The Classification of the Papilionidae Mainly Based on the Morphology of Their Immature Stages

Suguru IGARASHI

3–41, Shinoharakita-1, Kôhoku-ku, Yokohama-shi, 222 Japan

Introduction

There are a greater number of lepidopterists who have taken up classification of the family Papilionidae among the Rhopalocera. They based their theories on various aspects of adult morphology, that is, the wing venation, wing pattern, genitalia, antennae, legs, thorax and other parts. These have been improved upon by occasionally obtained information on the early stages, including the larval morphology and foodplants, and more recently, by studies of the chemistry of wing pigments.

In contrast, morphological studies on the early stages have not made as great progress, even though many scholars are fully aware of their importance in classification. It has been, and still is, extremely difficult to conduct systematic research on the early stages for the simple reason that it is generally very hard to secure larvae and pupae of these butterflies from across the world.

Fortunately, the author has been able to obtain first-hand information on the life histories of species of 30 genera out of the known 33 in the Papilionidae, and succeeded in collecting early stage specimens of these butterflies.

This paper aims at supplying more data on the early stages, with emphasis on larval morphology, adult habits and larval foodplants, as criteria for reviewing past classification. As a result of the present study, the author proposes partial revision of the past theories as well as their corroboration, and new classification of the Papilionidae.

Table 1. The species marked with white circles are those which were either reared by him or obtained as immersed or dried specimens; those marked with P indicate photographic reference or pictures drawn from life, and those with L, descriptions in literature or other illustrations.

	Specific Name	Egg	Larva 1	2	3	4	5	Pupa	
1.	*Baronia brevicornis*	P	○	○	○	○	○	○	Sent from VÁZQUEZ, L. & PÉREZ, H.
2.	*Luehdorfia japonica*	○	○	○	○	○	○	○	
3.	*L. puziloi*	○	○	○	○	○	○	○	
4.	*L. chinensis*						P	○	Sent from CHUAN-LUNG, LEE
5.	*Parnalius polyxena*	○	○	○	○	○	○	○	
6.	*P. rumina*	○	○	○	○	○	○	○	

蝶と蛾 *Tyô to Ga*, **34** (2): 41–96, 1984

Table 1. (Continued)

	Specific Name	Egg	Larva 1	2	3	4	5	Pupa	
7.	*Parnalius cerisy*	○	○	○	○	○	?	○	
8.	*Hypermnestra helios*	○	○	○	○	○	○	○	
9.	*Archon apollinus*	○	○	○	○	○	○	○	
10.	*Sericinus montela*	○	○	○	○	○	○	○	
11.	*Parnassius glacialis*	○	○	○	○	○	○	○	
12.	*P. stubbendorfii*	○	○	○	○	○	○	○	
13.	*P. mnemosyne*	○	○				L		HANS KONWICZKA Schmetterlinge, Pl. 2.
14.	*P. eversmanni*	○	○	○	○	○	○	○	
15.	*P. honrathi*							○	
16.	*P. bremeri*	○	○	○	○	○	○	○	
17.	*P. apollo*	○	○	○	○	○	○	○	
18.	*P. hardwickei*						○		
19.	*P. smintheus*						L		GATES CLARKE, J. F., 1962. Butterflies, 20.
20.	*P. autocrator*	○						○	
21.	*Cressida cressida*	○	○	○	○	○	○	○	
22.	*Euryades corethrus*						L	○	MUNROE, E., 1960. The classification of the Papilionidae (Lepidoptera) *Canad. Ent. Suppl.*, 17: 38
23.	*Battus philenor*	○			L		○	○	GATES CLARKE, J. F., 1962 Butterflies, 14.
24.	*B. polydamas*						L	L	OTHMAR DANESCH, 1965. Schmetterlinge 1, Tagfalter. 134, 135.
25.	*Pachliopta aristolochiae*	○	○	○	○	○	○	○	
26.	*P. polydorus*	○					○	○	
27.	*P. polyphontes*	○	○	○	○	○	○	○	
28.	*P. mariae*							○	
29.	*P. phegeus*		○	○	○	○	○	○	
30.	*P. atropos*	○	○	○	○	○	○	○	
31.	*P. coon*		○	○	○	○	○	○	
32.	*P. neptunus*							○	
33.	*P. hector*	○							
34.	*Atrophaneura semperi*	○	○	○	○	○	○	○	
35.	*A. horishana*	○	○	○	○	○	○	○	
36.	*A. aidoneus*							L	MELL, R., 1938. Beiträge zur Fauna Sinica. *Deut. ent. Zeit. Jahrg.*, 2: 285, Pl. 7, 8.
37.	*A. varuna*		○	○	○	○	○	○	
38.	*A. nox*	○	○	○	○	○	○	○	
39.	*A. hageni*		○	○	○	○	○	○	
40.	*A. dixoni*						L	L	STRAATMAN, R., 1968. *Ent. Ber. Amst.*, 28: 229, Pl. 6.

Table 1. (Continued)

	Specific Name	Egg	Larva					Pupa	
			1	2	3	4	5		
41.	*Atrophaneura alcinous*	○	○	○	○	○	○	○	
42.	*A. febanus*		○	○	○	○	○	○	
43.	*A. polyeuctes*	○	○	○	○	○	○	○	
44.	*A. dasarada*	○	○	○	○	○	○	○	
45.	*A. latreillei*	○	○	○	○	○	○	○	
46.	*Pharmacophagus antenor*						L	○	MABILLE, P., 1887. *in* GRANDIDIER, Hist. phys. nat. pol. Madagascar. 18, Lép., 1: 364.
47.	*Troides aeacus*	○	○	○	○	○	○	○	
48.	*T. rhadamanthus*	○	○	○	○	○	○	○	
49.	*T. magellanus*	○	○	○	○	○	○	○	
50.	*T. helena*	○	○	○	○	○	○	○	
51.	*T. hariphron*	○	○	○			○		
52.	*T. amphrysus*	○	○	○	○	○	○	○	
53.	*T. cuneifera*		○	○	○	○	○	○	
54.	*T. miranda*		○	○	○	○	○	○	
55.	*T. hypolitus*	○	○	○	○	○	○	○	
56.	*Trogonoptera brookiana*	○	○				○	○	
57.	*Ornithoptera priamus*	○	○	○	○	○	○	○	
58.	*O. croesus*		P	P	P	P	P	P	Sent from BORCH H.
59.	*O. paradisea*	P	P	P	P	P	P	P	Sent from STRAATMAN, R.
60.	*O. meridionalis*			P			P	P	Sent from STRAATMAN, R.
61.	*O. goliath*	P	P				P	P	Sent from STRAATMAN, R.
62.	*O. chimaera*	P	P				P	P	Sent from STRAATMAN, R.
63.	*O. victoriae*			P			P	P	Sent from STRAATMAN, R.
64.	*O. alexandrae*		P				P	○	Sent from STRAATMAN, R.
65.	*Chilasa epycides*	○	○	○	○	○	○	○	
66.	*C. slateri*		○	○	○	○	○	○	
67.	*C. clytia*	○	○	○	○	○	○	○	
68.	*C. agestor*	○	○	○	○	○	○	○	
69.	*C. paradoxa*						L	L	TALBOT, G., 1936. Fauna of British India, Butterflies, 1: 112.
70.	*C. toboroi*					P	P	P	Sent from STRAATMAN, R.
71.	*C. laglaizei*	P	P		P	P	P	○	Sent from STRAATMAN, R.
72.	*C. anactus*	○	○	○	○	○	○	○	
73.	*C. anchisiades*	○	○	○	○	○	○	○	

Table 1. (Continued)

	Specific Name	Egg			Larva			Pupa	
			1	2	3	4	5		
74.	*Agehana maraho*	○	○	○	○	○	○	○	
75.	*A. elwesi*						L	L	MELL, R., 1938. Beiträge zur Fauna Sinica. *Deut. ent. Zeit. Jahr.*, 2: 316.
76.	*Papilio machaon*	○	○	○	○	○	○	○	
77.	*P. hospiton*			L		L			GOODDEN, R., 1977. Monde Merveilleux des Papillons, 9.
78.	*P. alexanor*	○	○	○	○	P	P	○	
79.	*P. zelicaon*						○	○	
80.	*P. bairdii*	○	○	○	○	○	○	○	
81.	*P. rudkini*	○	○	○	○	○	○	○	
82.	*P. polyxenes*	○	○	○	○	○	○	○	
83.	*P. indra*						L		THOMAS, C. EMMEL Butterflies, 35.
84.	*P. xuthus*	○	○	○	○	○	○	○	
85.	*P. demoleus*	○	○	○	○	○	○	○	
86.	*P. demodocus*	L	L	L	L	L	L	L	VAN SON, G., 1949. The Butterflies of Southern Africa, 1: 20–24, Pl. 9.
87.	*P. ophidicephalus*	L	L	L	L	L	L	L	VAN SON, G., 1949. The Butterflies of Southern Africa, 1: 24–30, Pl. 10.
88.	*P. demolion*	○	○	○	○	○	○	○	
89.	*P. liomedon*	○					○	○	
90.	*P. gigon*	○	○	○	○	○	○	○	
91.	*P. cresphontes*						L		GATE CLARKE, J. F., 1962. Butterflies, 15.
92.	*P. thoas*						L		OTHMAR DANESCH, 1965. Schmetterlinge 1, Tagfalter, 121–123.
93.	*P. glaucus*	○	○	○	○	○	○	○	
94.	*P. rutulus*							○	
95.	*P. echerioides*	L	L	L	L	L	L	L	VAN SON, G., 1949. The Butterflies of Southern Africa, 1: 15–17, Pl. 8.
96.	*P. scamander*					○	○		OTHMAR DANESCH, 1965. Schmetterlinge 1. Tagfalter. 90, 91.
97.	*Euchenor euchenor*	○	○	P	P	P	○	○	Sent from STRAATMAN, R., MATSUKA, K.
98.	*Menelaides protenor*	○	○	○	○	○	○	○	
99.	*M. macilentus*	○	○	○	○	○	○	○	
100.	*M. bootes*							○	
101.	*M. thaiwanus*			○	○	○	○	○	
102.	*M. memnon*	○	○	○	○	○	○	○	
103.	*M. polymnestor*	○	○	○	○	○	○	○	
104.	*M. ascalaphus*	○	○	○	○	○	○	○	
105.	*M. rumanzovia*	○	○	○	○	○	○	○	

Table 1. (Continued)

Specific Name	Egg	Larva					Pupa	
		1	2	3	4	5		
106. *Menelaides helenus*	○	○	○	○	○	○	○	
107. *M. sataspes*					○	○	○	
108. *M. iswara*	○	○						
109. *M. polytes*	○	○	○	○	○	○	○	
110. *M. ambrax*						○	○	
111. *M. aegeus*	○	○	○	○	○	○	○	
112. *M. amynthor*						○	○	
113. *M. nephelus*	○	○	○	○	○	○	○	
114. *M. castor*	○	○	○	○	○			
115. *M. dravidarum*						L	L	Talbot, G., 1936. Fauna of British India, Butterflies, 1: 160, Pl. 1.
116. *M. lowi*		P	P	P	P	P	P	Sent from Tanaka, K.
117. *M. iswaroides*						○	○	
118. *Achillides fuscus*	○	○	○	○	○	○	○	
119. *A. hipponous*						P	P	Sent from Ae, S.
120. *A. canopus*						L		Common, I. F. B. & Waterhouse, D. F. 1972. Butterflies of Australia. 181, 182, Pl. 8.
121. *A. bianor*	○	○	○	○	○	○	○	
122. *A. polyctor*	○	○	○	○	○	○	○	
123. *A. maackii*	○	○	○	○	○	○	○	
124. *A. dialis*	○	○	○	○	○	○	○	
125. *A. krishna*	○	○	○	○	○	○	○	
126. *A. arcturus*	○	○	○	○	○	○	○	
127. *A. hoppo*						P	P	Sent from Ae, S.
128. *A. paris*	○	○	○	○	○	○	○	
129. *A. palinurus*	○	○	○	○	○	○	○	
130. *A. buddha*						L	L	Talbot, G., 1936. Fauna of British India, Butterflies, 1: 156–157, Pl. 1.
131. *A. blumei*	○	○						
132. *A. peranthus*	○	○	○	○	○	○	○	
133. *A. lorquinianus*			○	○	○	○	○	
134. *A. ulysses*	○	○	○	○	○	○	○	
135. *A. nireus*	L	L	L	L	L	L	L	Van Son, G., 1949. Butterflies of Southern Africa, 1: 30–33. Pl. 11.
136. *Pterourus troilus*	○	○	P	P	P	○	○	Sent from Ae, S.
137. *Meandrusa payeni*	○	○	○	○	○			
138. *M. gyas*	○	○						
139. *Teinopalpus imperialis*	○							
140. *Protographium leosthenes*	P	P				P	○	Sent from Nada Sankowsky
141. *Iphiclides podalirius*	○	○	○	○	○	○	○	
142. *Pathysa antiphates*						○	○	

Table 1. (Continued)

Specific Name	Egg	Larva 1	2	3	4	5	Pupa	
143. *Pathysa nomius*						L	L	TALBOT, G., 1936. Fauna of British India. Butterflies. 1: 207, Pl. 1.
144. *Pazala eurous*	○	○	○	○	○	○	○	
145. *Lamproptera meges*			○			○	○	
146. *L. curius*	○	L	○	○	○	○	○	HOWARTH, T. G., 1976. *J. Res. Lepid.*, 15 (1): 27–32.
147. *Graphium sarpedon*	○	○	○	○	○	○	○	
148. *G. cloanthus*	○	○	○	○	○	○	○	
149. *G. codrus*			○	○		○	○	
150. *G. doson*	○	○	○	○	○	○	○	
151. *G. eurypylus*					○	○	○	
152. *G. agamemnon*	○	○	○	○	○	○	○	
153. *G. macfarlanei*	○	○	○	○	○	○	○	
154. *G. morania*	L	L	L	L	L	L	L	VAN SON, G., 1949. The Butterflies of Southern Africa, 1: 37–39, Pl. 12.
155. *G. leonides*	L	L	L	L	L	L	L	VAN SON, G., 1949. The Butterflies of Southern Africa, 1: 39–42, Pl. 13.
156. *G. policenes*	L	L	L			L	L	VAN SON, G., 1949. The Butterflies of Southern Africa, 1: 45–49, Pl. 14.
157. *G. macleayanum*	○	○	○	○	○	○	○	
158. *G. evemon*						L		ALEXANDER B. KLOTS & ELSIE B. KLOTS, 1959. Living Insects of the World, 185.
159. *Eurytides marcellus*	○	○	○	○	○	○	○	

Historical Review on Classification of Papilionidae

GOSSE 1881: Subdivided the family into *Troides*, *Pachliopta*, *Papilio* and *Graphium* on the basis of the morphology of the valva of the male genitalia.

STAUDINGER & SCHATZ 1892: Regarded *Euryades* and *Cressida* as the most primitive.

JORDAN & STICHEL 1907: Regarded *Baronia* as allied to *Parnassius*.

EIDMANN 1930: Adopted female genitalia as criterion for classification.

YASUMATSU & TORIGATA 1934: Classified Japanese Papilionids (including some from Taiwan) according to the features of male genitalia.

TALBOT 1936: Adopted early stages, male genitalia and wing venation as criteria for classification.

ZEUNER 1943: Studied the wing venation in the Troidini found in the Australasian Archipelago with emphasis on the flap of the male hindwing, and discussed their distribution and phylogeny in relation to zoogeography.

FORD 1944: Introduced chemical analysis of wing pigments into classification, making it more convincing; regarded *Euryades* and *Cressida* as the most primitive; denied the generic status of *Chilasa*; interpreted as secondary specialization the absence of sent scales on the flap of the male hindwing in the Papilionini; considered *Teinopalpus* to be an extremely specialized group of Papilionini, subdivided the Zerynthiini into the *Luehdorfia-Zerynthia* Group and the *Sericinus-Bhutanitis* Group, considering them to have specialized in opposite directions; opposed STICHEL's view (1907) that *Archon* is an intermediate between *Zerynthia* and *Parnassius*.

SHIRÔZU 1955: Gave *Chilasa* the status of an independent genus; opposed FORD's division of the Zerynthiini, but agreed to his view that *Luehdorfia* is the most primitive among the Zerynthiini; supported STICHEL's view on *Archon* as an intermediate between *Zerynthia* and *Parnassius*; opposed FORD's interpretation of the absence of androconia in the hindwing flap in the Papilionini, regarding it as retention of a primitive feature rather than secondary specialization; divided the Troidini into *Battus*, *Troides* and *Atrophaneura*.

EHRLICH 1958: Defined the three subfamilies of Papilioninae, Parnassiinae and Baroniinae from the viewpoint of adult morphology.

MUNROE 1960: Classified the family primarily on the basis of the antennae, legs, wing venation and morphology of the genital organs of both sexes, using available information on early stages, larval foodplants and distribution as supporting evidence; divided the Papilionidae into three subfamilies of Parnassiinae, Baroniinae and Papilioninae; proposed that *Archon* should be associated with *Zerynthia*, regarding the pupal structure as only a secondary feature; left the question of comparative primitiveness open between the Troidini with dark larvae having fleshy tubercles and the Leptocircini with smooth, greenish larvae; included *Chilasa* in *Papilio*.

HIURA 1980: Proposed separation of *Hypermnestra* from the Parnassiini based on his analysis of the wing patterns in the Parnassiinae, to make *Hypermnestra* an independent tribe.

These authors appear to be in broad agreement on the following points, namely:

1. Exclusion of *Baronia* from any of the main branches of the phylogenetic tree to assign it to a separate branch.
2. Recognition of the Zerynthiini and Troidini, whose larval hosts are predominantly aristolochiaceous plants, as more primitive groups.
3. And *Cressida* and *Euryades* as the most primitive among them.
4. Inclusion of *Chilasa* in *Papilio*, except by TALBOT and SHIRÔZU, who regarded the former as an independent genus.
5. Inclusion of the *machaon*-, *polytes*- and *bianor*-groups in a single genus *Papilio*, rather than their separation.
6. No reference to the position of *Meandrusa*, or inclusion of it in the Leptocircini.
7. Recognition of *Teinopalpus* as an extremely specialized genus.

Here is reproduced a phylogenetical tree proposed by FORD (1944) incorporating the just-mentioned factors.

The author deems it necessary to effect some important changes in the current classification of the Papilionidae, when it is compared with newly-obtained data on

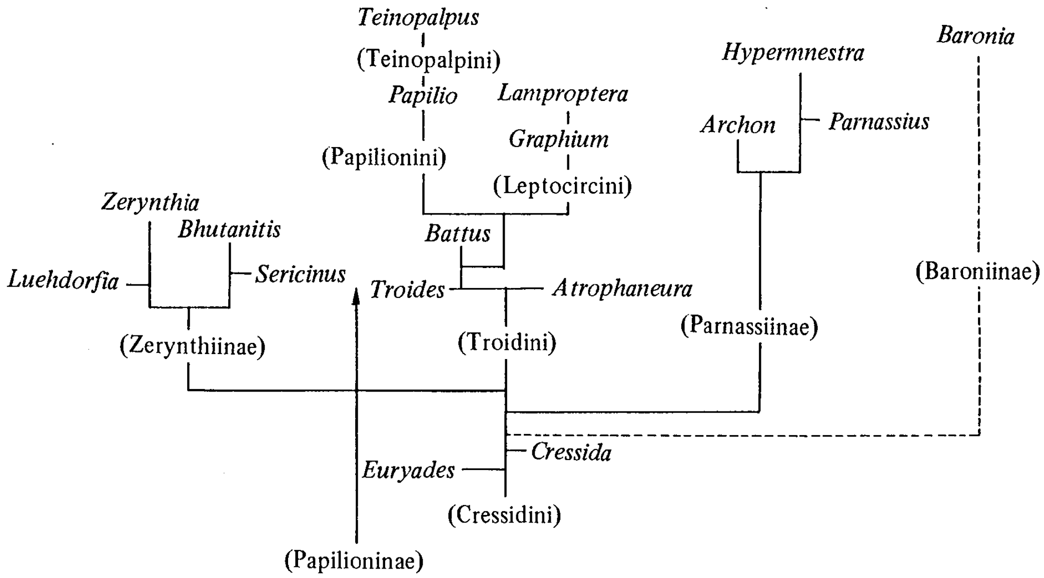


Fig. 1. Phylogenetic relationships of the Papilionidae proposed by FORD (1944).

early stages, especially the results of their detailed morphological studies.

The particular features of the early stages studied by the author will be discussed in the chapters to follow.

Morphology

Eggs

Eggs of Papilionid species fall under one of the following three categories.

a. Smooth spherical type

Luehdorfia, *Parnalius*, *Archon*, *Sericinus*, *Hypermnestra*, *Papilio*, *Euchenor*, *Menelaides*, *Achillides*, *Agehana*, *Lamproptera*, *Meandrusa*, *Pazala*, *Pathysa*, *Graphium*, *Iphiclides* and *Protographium*.

b. Coarse flat-shaped type

Parnassius

c. Granulated spherical type

Cressida, *Battus*, *Atrophaneura*, *Pachliopta*, *Troides*, *Ornithoptera* and *Chilasa*.

Larvae

a. Setae on the head of the first-instar larva

Papilionid larvae can be classified according to the number and distribution pattern of the setae on the head as follows.

a–1. Primitive type

Luehdorfia, *Parnalius*, *Hypermnestra*, *Archon*, *Sericinus*, *Parnassius*, *Troides*, *Ornithoptera*, *Meandrusa* and *Graphium*, with least numbers of primary setae.

a–2. Semi-advanced type

Cressida, *Pachliopta*, *Chilasa*, *Agehana* and *Atrophaneura*, with more setae or dots added to the primitive pattern.

a–3. Advanced type

Baronia, *Papilio*, *Menelaides*, *Achillides and Iphiclides*, with numerous setae from which the counterparts of the setae of the primitive type cannot be distinguished.

It appears as if the number of setae increases with evolution, but this falls short of being an effective criterion for all genera because of not infrequent exceptions. These include *Baronia*, a primitive species with numerous furcate setae on the head, and *Meandrusa* or *Graphium* with all advanced characteristics except their primitive head setae.

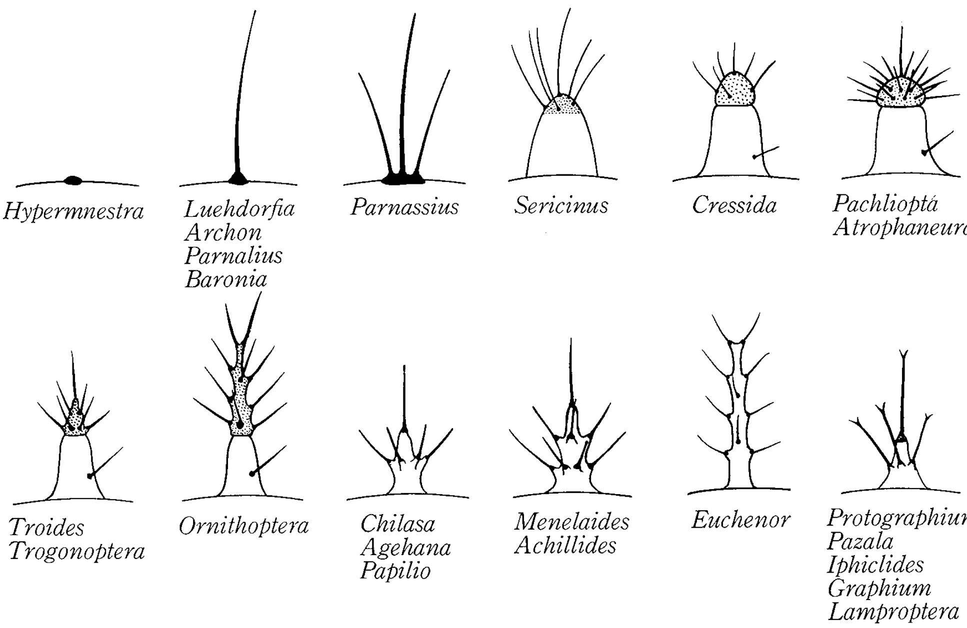


Fig. 2. Tubercles and setae on the dorsal area of body segments of the first-instar larvae.

b. Setae and tubercles on the body of the first-instar larva

In classification, the most primitive feature or features in a species' morphology offer important clues. Eggs are too simple in exterior structure, and observation of the embryonic development within the chorion is not generally feasible. As a result, attention has been focused on the morphology or external features of the first-instar larva.

A close study of the second to the final larval instar in a species will show that the larval colouring and morphology, if not the dimensions, do not change very greatly from instar to instar. Yet every first-instar larva greatly differs in morphology from the larvae of the same species in the second and later instars. A conventional idea of perfect metamorphosis places all larval instars under one category, but the features of the first-instar larva may well call for one distinct rubric; thus, it will be safe to propose a complete metamorphosis of a butterfly consisting of the stages of the egg, first-instar larva, larva of any other instar, pupa and adult.

All the setae and tubercles of any first-instar larva occur in even numbers, and in

symmetry. Even though older larvae of such nymphalid species as *Nymphalis xanthomelas*, *Cyrestis thyodamas* and *Araschnia burejana* each carry a dorsal row of spines or single projections, their first-instar larvae are without trace of these. It is doubtful whether there exists at all a first-instar larva provided with an odd number or setae or asymmetrical projections. The occurrence of setae in even numbers indicate that the first-instar larva is the final result of embryonic cell division that has progressed in terms of the nth power of two.

After the first ecdysis, seemingly insignificant setae and/or projections make their appearance in such a manner as would make it difficult for us to distinguish between evolution and specialization. Pupae may develop still more puzzling dents and projections whose evolutionary significance is hard to assess.

However, there do seem to exist a few measures for evaluating the degree of evolution in a species, derived from comparison between larval morphology and larval habits, foodplants, oval and pupal characteristics and adult features including colouring and pattern. They are, for instance:

b–1. Simple first-instar morphology suggests primitiveness, and the reverse seems true; the primary setae on the body tend to be less in number in primitive species, and more in advanced species. But this criterion is not valid as far as the setae on the head are concerned.

b–2. Greater morphological changes during the whole larval stage appear to be seen in more advanced species.

b–3. Faster morphological changes during the total larval period also seem to suggest more advanced stages in evolution.

c. Osmeterium

This fleshy organ proper to larvae of this family is believed to have developed from the skin in front of the prothoracic plate. Normally it is hidden, being retracted just under the thoracic skin. It is lined with glands secreting a liquid of a pungent smell. The tubular organ is everted forward at a stimulus, its exposed surface being wet with the secretion. In *Luehdorfia*, *Parnalius*, *Archon*, *Hypermnestra*, *Parnassius*, *Sericinus*, *Cressida*, *Pachliopta*, *Atrophaneura*, *Troides*, *Ornithoptera* and others, the osmeterium is short and not well developed. Their larvae do not show any sensitive reaction to stimulus so far as the protrusion of the osmeterium is concerned. The first-instar larva of *Archon* or *Parnassius* does not protrude this organ. In contrast, larvae of

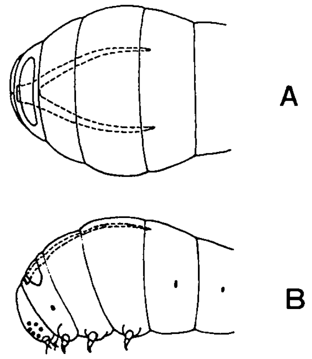


Fig. 3. Osmeterium in retracted condition. A: Dorsal aspect. B: Lateral aspect.

Chilasa, *Papilio*, *Menelaides*, *Achillides*, *Meandrusa*, *Lamproptera*, *Pazala*, *Graphium* etc. are equipped with a long, well developed organ, which they extrude at slightest stimuli. They often sway or raise their bodies at the same time.

Osmeterial development thus appears to serve as a criterion.

d. Thoracic form

A humped thorax is a conspicuous feature in *Papilio*, *Menelaides*, *Achillides*, *Meandrusa*, *Iphiclides*, *Lamproptera*, *Pazala*, *Graphium* and others. In contrast, larvae of *Baronia*, *Archon*, *Hypermnestra*, *Parnassius*, *Luehdorfia*, *Parnalius*, *Sericinus*, *Battus*, *Cressida*, *Pachliopta*, *Atrophaneura*, *Troides*, *Trogonoptera*, *Ornithoptera* and *Chilasa* are more or less uniformly cylindrical. Hence, a humped thorax seems to show an advanced stage in evolution.

e. Larval colouring and pattern

The larvae of the most primitive papilionid species would undoubtedly have been dark-coloured, judging from the fact that almost all first-instar larvae are dark brown to black. It can safely be said that species with dark final-instar larvae are more primitive, even though there may be exceptions. However, larval colouring and pattern, unlike setae and projections, appear to be subject to comparatively quick change according to the environment, and these alone should not always be relied upon as criteria.

The white or pale diagonal dorsal patch on the third and fourth abdominal segments, often referred to as a saddle mark, is present in species at fairly advanced stages of evolution. It occurs quite commonly, as in *Cressida*, *Pachliopta*, *Atrophaneura*, *Troides*, *Trogonoptera*, *Ornithoptera*, *Chilasa*, *Agehana*, *Papilio*, *Menelaides*, *Achillides*, *Meandrusa* and others. It is absent in *Iphiclides* (except for the first-instar larva), *Lamproptera*, *Pazala* and *Graphium*. The saddle mark was possibly lost in the latter group as a result of further evolution.

Pupae

a. Projections

The pupal body retains traces of larval tubercles, prothoracic and anal plates and prolegs in some form or other. Some pupal projections closely resemble the corresponding larval tubercles, but the latter can also be reduced, more often than not, to markings of different colouring. Generally speaking, pupae of more advanced species tend to be smooth-surfaced and have less projections. *Achillides* and *Graphium* are good examples. The prominent horn-like thoracic projection found in *Graphium* and related genera is a secondary development due to adaptation to the living environment, simulating as it does a petiole or peduncle of a fruit-bearing evergreen tree. In fact, there is not the slightest suggestion of the pupal horn on the dorsum of the mesothorax of even a mature larva.

However, the fact remains that there are primitive genera with smooth pupae, which are absolutely devoid of protuberances. These include *Hypermnestra*, *Archon* and *Parassius*. Again this is a case of adaptation to environment, as they pupate in cocoons spun on the ground or among the litter. Horns and knobs would have no place in narrow space such as the inside of cocoons.

b. Cremaster

This is a development and remnant of the anal plate of the larva. It is degenerate in *Hypermnestra*, *Archon*, *Parnassius* and others, whose larvae spin cocoons on or in the ground to pupate within. In other genera, the cremaster is well developed and presents no significant difference between genera. Those pupating in cocoons do not cast off their larval skins, and the pupae's caudal ends stay in the tucked-up exuviae. This is naturally a specialized feature.

c. Body colouring

The colouring of the pupa is roughly divided into two types: brown only and alternating between green and brown. To the former monochrome type belong *Luehdorfia*, *Archon*, *Hypermnestra*, *Parnalius*, *Sericinus*, *Parnassius*, *Baronia*, *Chilasa*, *Agehana*, *Pachliopta*, *Atrophaneura*, *Cressida* and others. The compatible type is represented by *Battus*, *Troides*, *Ornithoptera*, *Papilio*, *Menelaides*, *Achillides*, *Graphium*, *Pazala*, *Lamproptera* etc. Though there are some exceptions such as *Battus* and *Troides*, primitive genera are usually characterized by the occurrence of brown pupae only. On the other hand, there is but nominal compatibility in advanced genera such as *Graphium* and *Pazala*, whose brown-type pupae are comparatively rare.

Morphological change

How evolution may be reflected in morphology has been discussed in the preceding chapters, and now this question is taken up from a different angle. It is agreed that, in other animals, loss of ancestral characteristics occur at earlier stages of development in the case of more advanced species, and that more primitive species retain such features until later stages.

Indeed studies on male genitalia, wing venation, antennae and legs in papilionids have been carried out since many years ago as criteria for evolutionary changes, but relatively few attempts have been made to find these among the features of early stages. The present author has made note of morphological changes in larval tubercles and setae and analyzed these, as tabulated in Fig. 4. If these changes are evaluated in the light of the afore-mentioned principle established for other forms of organisms, we may be able to discuss evolution in Papilionidae in terms of the changes involving larval tubercles or projections — whether they develop or disappear. Thus it follows that greater changes in tubercles and/or setae occur in more advanced species, and vice versa. This principle is in perfect conformity with the other morphological evolutionary features so far discussed.

Habits

The Papilionidae are also known for the diversified ecological features of their early stages, especially of the larvae. While more advanced species thriving in environments with abundant vegetation and warm climates lead more or less similar lives, by far the more specific aspects are found in the lives of primitive species adapted to much less favourable surroundings — arctic or arid, for example. It is often the latter group of butterflies that offer valuable clues for the study of evolution.

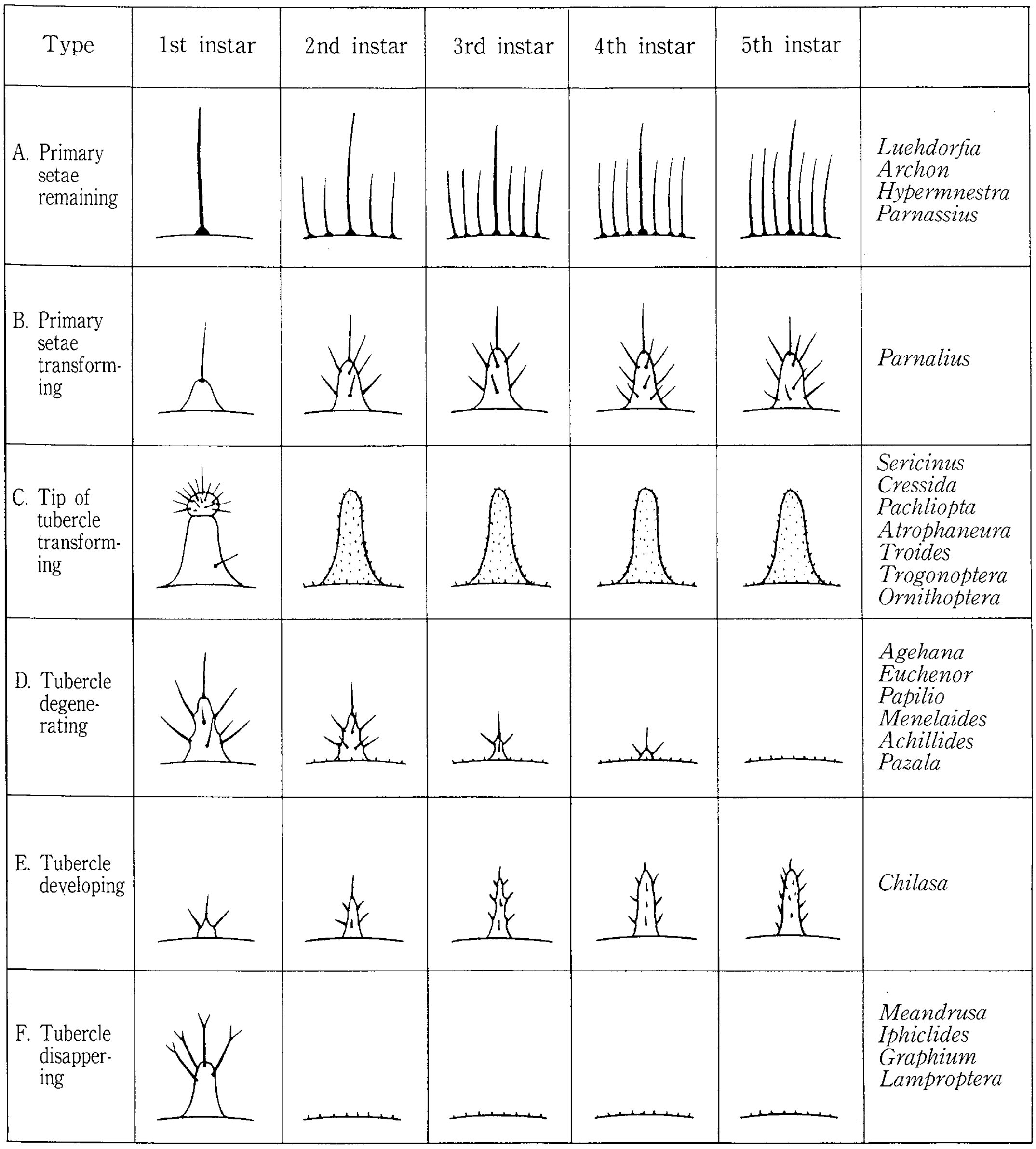


Fig. 4. Aspects of change in larval setae and tubercles on the dorsal area of body segments.

Larval habits

a. Hibernation as eggs

Most of the *Parnassius* species whose life histories are known pass the winter as eggs. Strictly speaking, however, this is a special form of overwintering as larvae. That is, the eggs deposited in summer quickly develop and the embryonic development completes long before the winter. The larvae stay within the eggshell all the time, without attempting to eat their way out before the following spring.

b. Position at rest

Larvae of *Luehdorfia*, *Sericinus*, *Pachliopta*, *Atrophaneura*, *Troides*, *Ornithoptera*, *Lamproptera* etc. keep to the underside of the leaf of foodplant. *Archon* larvae seek cover among leaves bound together with silk, or burrow into flowers or fruits of *Aristolochia*. The two contrastive resting habits appear to indicate that preference for the

underside spells primitiveness. The exceptions include *Parnalius* and *Hypermnestra*, whose larvae sit on the upperside of the leaf.

c. Gregariousness

Larvae resulting from eggs laid in batches usually remain gregarious, feeding and resting in unison. This habit is recognized in larvae of *Luehdorfia*, *Archon*, *Parnalius*, *Sericinus*, *Atrophaneura*, *Chilasa* and others, and also in *Troides* and *Ornithoptera*, though less conspicuously. Throughout their larval period, remarkably strong gregariousness is seen in *laglaizei*, *toboroi* and *anchisiades*, which were formerly placed in *Papilio*. Recent studies have also shown that these should belong to *Chilasa*.

The larvae of *Papilio*, *Menelaides*, *Achillides*, *Iphiclides*, *Pazala*, *Graphiun* and others are solitary. Thus, larval gregariousness should be regarded as a primitive character.

Mode of pupation

The pupae of archetype papilionids may in all probability have been girdled, as those of a majority of the existing species are. So far, three variations have been known.

a. Head-and-tail supporting type

Parnalius is known for this remarkable feature. There is a barbed hook at the extremity of the pupal head, which catches a silk strand. However, this support by the head is nothing but a result of transfer of a normally spun silk girdle, which the pupa effects some time after pupation by twisting and turning its body. We can call this a special case of the normal mode.

b. Thoracic girdle type

This is seen in a majority of papilionids. The silk girth is deeply embedded in the pupal skin.

c. Cocoon-spinning type

Three genera, *viz. Hypermnestra*, *Archon* and *Parnassius*, belong to this category. The former two larvae burrow rather deeply in the ground before they spin up for pupation. Larvae of the last-named either utilize fallen leaves or creep between stones to find space for spinning cocoons. These habits are unusual among butterflies but may be interpreted as adaptation to rigorous environments: arid climates in the case of the former and arctic climates for the latter.

Number of broods per year

a. Univoltine

Luehdorfia, *Parnalius*, *Archon*, *Hypermnestra*, *Parnassius*, *Chilasa* (not all) and *Pazala*.

b. Multivoltine

Sericinus, *Battus*, *Cressida*, *Pachliopta*, *Atrophaneura*, *Troides*, *Ornithoptera*, *Agehana*, *Euchenor*, *Papilio*, *Menelaides*, *Achillides*, *Iphiclides*, *Meandrusa*, *Teinopalpus*, *Lamproptera* and *Pathysa*.

Archetype papilionids were evidently univoltine, because primitive species are now mostly confined to arctic, subarctic, alpine or arid regions. More advanced, and

therefore successful, species avail themselves of abundant foodplants in the tropical, subtropical and torrid zones and tend to be multivoltine. In such places, however, old, primitive species can also be multivoltine, having adapted to the favourable environment.

Flight habits

It is easy to see that faster fliers have a greater chance of escaping from predation by other animals. The agility of adults in flight certainly contributes to their safety, although their survival does not solely depend on it.

When similar groups of insects are compared, advanced species generally fly faster than primitive ones.

Among the woodland hairstreaks of Japan, *Japonica lutea*, *Artopoetes pryeri* and other more primitive species are either slow or monotonous in flight in comparison with more advanced representatives such as *Chrysozephyrus ataxus* and *Favonius orientalis*.

Naturally, there are exceptions to this rule: mimetic butterflies, however advanced, tend to fly as slowly as the unpalatable models.

Comparison of flying habits among various papilionids shows that the Zerynthiini, Parnassiini and Troidini whose larvae feed on aristolochiaceous plants are slow fliers, and that the Leptocircini whose larval foodplants mostly belong to the Lauraceae, Magnoliaceae and related families are rapid fliers.

a. Slow, linear, low flight
   Luehdorfia, *Parnalius*, *Hypermnestra*, *Archon*, *Parnassius*, *Sericinus*, *Cressida*, *Lamproptera*.
b. Slow, linear, medium to high flight
   Pachliopta, *Atrophaneura*, *Troides*, *Ornithoptera*, *Chilasa*, *Agehana*.
c. Vigorous, fluttering, high flight
   Papilio, *Euchenor*, *Menelaides*, *Achillides*, *Iphiclides*.
d. Rapid, skipping, medium to high flight
   Graphium, *Meandrusa*, *Pazala*.

A glance at these flight habits will readily show that such genera as are characterized by advanced morphology and habits excel in motility, and that primitive species tend to fly low and slowly. An enigmatic case in this connection is *Teinopalpus*. The male flies nearly as fast and energetically as *Graphium* spp., but the female has a slow, linear flight. In addition, the male, once it has settled, is apt to be as torpid as some moths in the daytime, not even responding to a finger touch. Therefore, no attempt is here made to draw any conclusion from the flight habits of *Teinopalpus*.

Adults' taste for water

Of all the known genera of the papilionid butterflies, only *Teinopalpus* does not have a flower-visiting habit. Both sexes of all other genera come to flowers for nectar. Some species are also known to be attracted to wet places, but this habit is almost exclusively confined to freshly emerged males of Papilionini and Leptocircini. The habit is probably absent in Zerynthiini, Parnassiini and Troidini, even though there is only one record of a male of *Luehdorfia japonica* visiting a wet place, and *Pachliopta*

aristolochiae was also seen by a puddle in Borneo.

Also, too well-known an exception is *Trogonoptera brookiana*, whose males swarm to waterside to drink. Predilection of fresh males for moisture can possibly be an advanced type of behaviour.

Table 2. Water drinking habit of the Papilionidae.

Subfamily	Tribe	Genus	Water drinking habit
Baroniinae		*Baronia*	
Zerynthiinae	Zerynthiini	*Luehdorfia*	Exceptional
		Parnalius	
		Sericinus	
		Bhutanitis	
	Parnassiini	*Archon*	
		Hypermnestra	
		Parnassius	
Papilioninae	Troidini	*Battus*	Occasional
		Cressida	
		Euryades (?)	None
		Parides	
		Pachliopta	Occasional
		Atrophaneura	
		Troides	
		Trogonoptera	Frequent
		Ornithoptera	
		Pharmacophagus (?)	
	Papilionini	*Chilasa*	
		Agehana	
		Papilio	
		Euchenor	
		Menelaides	
		Achillides	
		Meandrusa	
	Leptocircini	*Protographium*	Existent
		Iphiclides	
		Lamproptera	
		Pathysa	
		Pazala	
		Graphium	
		Eurytides	
		Teinopalpus	

Table 3. Larval foodplants of the Papilionidae.

<table>
<tr><th>Subfamily</th><th>Tribe</th><th>Genus</th><th colspan="2">Foodplants</th></tr>
<tr><td>Baroniinae</td><td></td><td>Baronia</td><td colspan="2">Fabaceae</td></tr>
<tr><td rowspan="4">Zerynthiinae</td><td>Zerynthiini</td><td>Luehdorfia
Parnalius
Sericinus
Bhutanitis (?)</td><td></td><td rowspan="6">Aristolochiaceae</td></tr>
<tr><td rowspan="3">Parnassiini</td><td>Archon</td><td></td></tr>
<tr><td>Hypermnestra</td><td>Zygophyllaceae</td></tr>
<tr><td>Parnassius</td><td>Papaveraceae
Crassulaceae</td></tr>
<tr><td rowspan="15">Papilioninae</td><td rowspan="2">Troidini</td><td>Battus
Cressida
Euryades
Parides
Pachliopta
Atrophaneura
Troides
Trogonoptera
Ornithoptera</td><td></td></tr>
<tr><td>Pharmacophagus</td><td>Combretaceae</td></tr>
<tr><td rowspan="5">Papilionini</td><td>Chilasa</td><td>Lauraceae, Rutaceae</td><td rowspan="13">Rutaceae
Annonaceae
Magnoliaceae
Lauraceae</td></tr>
<tr><td>Agehana</td><td>Lauraceae</td></tr>
<tr><td>Papilio</td><td>Apiaceae, Rutaceae etc.</td></tr>
<tr><td>Euchenor
Menelaides
Achillides</td><td>Rutaceae</td></tr>
<tr><td>Meandrusa</td><td>Lauraceae</td></tr>
<tr><td rowspan="8">Leptocircini</td><td>Photographium</td><td>Annonaceae</td></tr>
<tr><td>Iphiclides</td><td>Rosaceae</td></tr>
<tr><td>Lamproptera</td><td>Hernandiaceae</td></tr>
<tr><td>Pathysa</td><td>Annonaceae, Magnoliaceae</td></tr>
<tr><td>Pazala</td><td>Lauraceae</td></tr>
<tr><td>Graphium</td><td>Lauraceae, Annonaceae</td></tr>
<tr><td>Eurytides</td><td>Annonaceae</td></tr>
<tr><td>Teinopalpus</td><td>Thymelaeaceae
(Not reconfirmed)</td></tr>
</table>

The followings are additional comments on the Table 3 of foodplants, or inductions from its study.

a. An overwhelming majority of primitive papilionids rely on Aristolochiaceae as larval foodplants.
b. Semi-advanced groups such as *Papilio*, *Menelaides* and *Achillides* mostly feed on Rutaceae.
c. The most advanced Leptocircini, feeding on Magnoliaceae and Lauraceae, might have returned to these after a series of shifts.

Foodplants

Most authors who have classified the Papilionidae on the basis of adult morphology agree that *Aristolochia*-feeders are primitive species. The author's study on early stages supports this view, and he does not hesitate to regard *Aristolochia*-species as some of the foodplants of the ancestral papilionids.

The possible shift from these to Zygophyllaceae, Papaveraceae, Crassulaceae and others is considered to be a result of secondary specialization. It should be noted here that the dependence of an impressive number of primitive species on Aristolochiaceae, also primitive plants, is often overemphasized. When papilionids as seen today made their appearance, there must have been higher forms of phanerogams that made nectar available to these butterflies. Thus, by far the greater liberty of choice of foodplants by these ancestral butterflies would have existed; then it seems more logical for us to think that these primitive papilionids have come to feed on Aristolochiaceae by their own preference rather than for want of alternatives.

The next question concerns the status of the Leptocircini whose important larval foodplants belong to the Lauraceae and Magnoliaceae: whether they are more advanced or more primitive than the *Alistolochia*-feeders. Results of past morphological studies of the adults of the Leptocircini have revealed some characteristics that have puzzled the researchers. They have been unable to determine what such features signify — degeneration or primitiveness. Having examined their early stages, the author came to the conclusion that the Leptocircini include advanced genera except for *Protographium*. He believes that their dependence on some of the most primitive phanerogamous plants, Magnoliaceae, is not incompatible with this evaluation, because the evolution of an animal species does not necessarily proceed at the same rate as the advancement of its feeding habits. Examples of reversion in the choice of foodplants are known in other groups of Lepidoptera.

The followings are family names of the known foodplants of the Papilionidae.

1. Aristolochiaceae: *Luehdorfia*, *Archon*, *Parnalius*, *Sericinus*, *Cressida*, *Pachliopta*, *Atrophaneura*, *Trogonoptera*, *Troides*, *Ornithoptera*, *Battus*, *Euryades*, *Parides*.
2. Combretaceae: *Pharmacophagus*.
3. Zygophyllaceae: *Hypermnestra*.
4. Fabaceae: *Baronia*.
5. Papaveraceae: *Parnassius*.

6. Crassulaceae: *Parnassius*.
7. Apiaceae: *Papilio*.
8. Rutaceae: *Papilio*, *Euchenor*, *Menelaides*, *Achillides*.
9. Magnoliaceae: *Agehana*, *Graphium*.
10. Annonaceae: *Graphium*, *Pathysa*.
11. Lauraceae: *Chilasa*, *Agehana*, *Pazala*, *Graphium*, *Meandrusa*.
12. Monomiaceae: *Graphium*.
13. Rosaceae: *Iphiclides*.
14. Malvaceae: *Papilio* (*homerus*), *Graphium* (*codrus*).
15. Asteraceae: *Papilio*.
16. Salicaceae: *Papilio* (*glaucus* Group).
17. Betulaceae: do.
18. Tiliaceae: do.
19. Oleaceae: do.
20. Cannabiaceae: do.
21. Rhamnaceae: do.
22. Piperaceae: *Atrophaneura*, *Papilio* (*thoas*, *hectorides*).
23. Hernandiaceae: *Lamproptera*.

Definition of Various Genera

Baronia SALVIN 1893

Trans. ent. Soc. Lond. (4): 331

Egg: rather low dome-shaped, unlike any other papilionids excluding *Parnassius* having spherical eggs. (Fig. 5–A)

1st-instar larva: numerous bifurcate or trifurcate short setae found on the head, but their arrangement unlike that of any other papilionid; the body also thickly covered with normal hairs whose distribution is irregular and has nothing in common with that of any other papilionid. Yet, the larva does possess an osmeterium, an important criterion. (Fig. 5–B, C)

2nd- to last-instar larvae: each seta on the head with two to five branches. This feature is quite unknown in other papillionids.

Pupa: in general appearance resembling that of *Luehdorfia*, but the head slightly tilted towards the ventral side, giving the pupa a hump-backed form. (Fig. 5–D)

In cross section, the pupa is featured by five distinct angles (representing longitudinal ridges), as shown in Fig. 5–E. This contrasts with those of *Luehdorfia* and *Parnassius* which have roundish cross sections.

The mode of pupation has not been reported, but a close examination of pupal specimens failed to reveal evidence of a girdle being spun. Since it is known to pupate in a cavity made in the ground, the mature larva perhaps spins a loose cocoon and this may allow the larva to dispense with a girdle. The caudal extremity is provided with a crude cremaster. The existence of

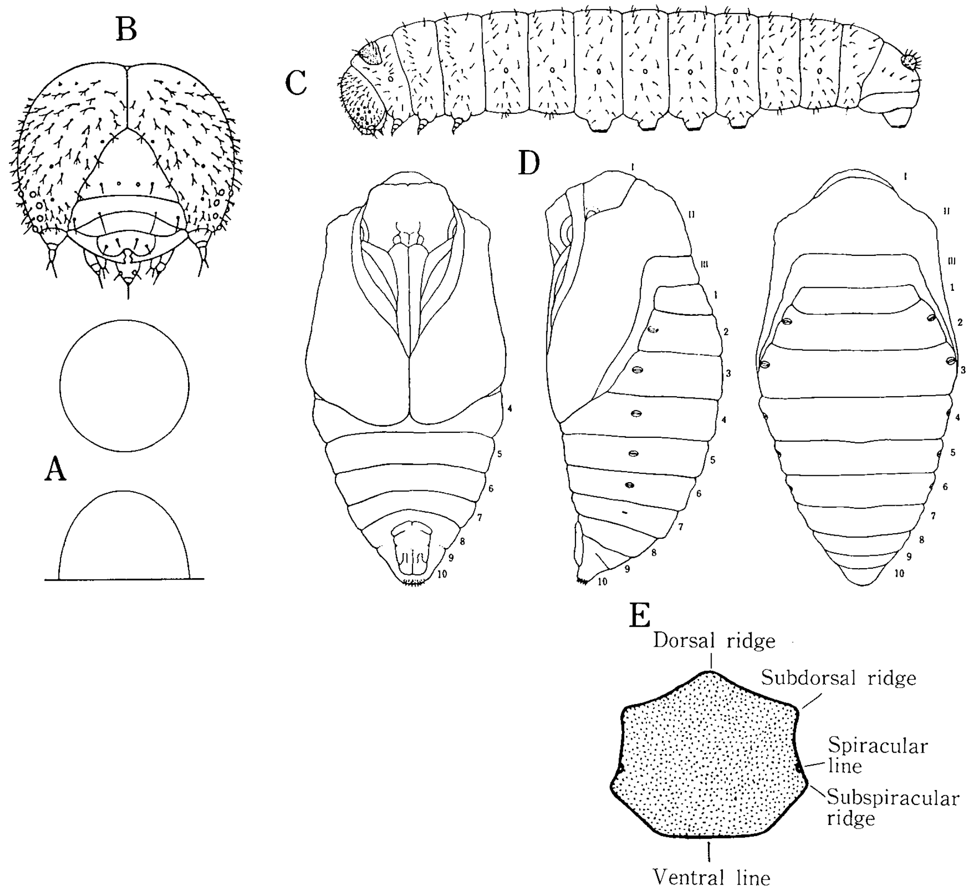


Fig. 5. *Baronia brevicornis*. A: Egg. B: Head of 1st instar, frontal view. C: First instar larva. D: Pupa (left, ventral view; middle, lateral view; right, dorsal view). E: Pupa, cross section.

the cremaster also makes the species distinct from *Archon*, *Hypermnestra* and *Parnassius*.

Adult: Vein 9 on the forewing absent, with veins 11 and 12 fused. These are remarkable specialized features of this species. The antennae are disproportionately short.

Foodplants: Fabaceae (*Acacia*).

Stage of the genus: its various unusual morphological characteristics have led to doubts about the validity placing this species under the Papilionidae.

Munroe (1960) observes: "Ford (1944), following Zeuner (1943), misinterpreted the homology of the anal veins of the papilionid hindwing, identifying 2nd and 3rd A of Baroniinae, Pieridae, and other Rhopalocera with 1st and 2nd A of Papilioninae. He therefore did not recognize the primitive character of the presence in *Baronia* of 3rd A, absent or rudimentary in all other Papilionidae. The preservation of this vein suggests that the Baroniinae diverged from the main papilionid stem below the level of any other existing form. The association of M_2 with cubitus, the basal approximation of 2nd and 3rd A of the forewing, and the preservation of the foretibial epiphysis mark *Baronia* as a papilionid; the male genitalia, too, are of

papilionid rather than pierid type. The short, naked antennae, the loss of one radial and anastomosis of another with Sc, the fusion of male ninth and tenth tergites and loss of socii, and the weakening of the distal portion of the valvae, are specialized characters that eliminate *Baronia* from consideration as a papilionid prototype. The relict distribution in western Mexico harmonizes with the primitive and isolated taxonomic position of the Baroniinae. Although BRYK's (1913, 1934) ranking of the group as a family does not violate taxonomic facts, it does tend to obscure rather than to clarify relationship and I accordingly follow FORD in retaining the Baroniinae in the Papilionidae as a subfamily. The early stages of *Baronia* are unknown. It will be interesting to see whether or not the larva has an osmeterium and red segmental tubercles, and whether the pupa is suspended by a girth." Absence of any information on the early stages of *Baronia* must have been frustrating to MONROE when he wrote this paper.

It is a remarkable coincidence that, in the next year, VÁZQUEZ and PÉREZ (1961) published an article on the immature stages and ecology of *Baronia brevicornis* SALVIN. Even though the larva and pupa of *Baronia* were accurately illustrated and described in the work, the present author at that time was yet to prepare reference materials of other papilionids for comparison. Fortunately, the author was able to compare *Baronia* with other species and to publish the result.

Recently, the Mexican scholars kindly met the author's request for larval specimens of all instars and pupae, plus their colour photographs. A close examination of these showed that the pupa has a cremaster but probably does not spin a girdle — a point not mentioned in their papers.

In conclusion, the present author favours a subfamily status for *Baronia*, despite the unique features of its early stages. *Baronia* after all belongs to the Papilionidae rather than to any other family, in view of the conspicuous differences found among the subfamilies of this group.

Luehdorfia CRUGER 1878

Verh. Nat. Ver. Ham. 3, p. 128 (Sep., p. 1)

Egg: spherical, pale green in colour with pearly lustre.

1st-instar larva: the number of the setae on the head one of the smallest among the papilionids, hence showing the basic pattern. This type of chaetotaxy is also found in *Parnalius*, *Hypermnestra*, *Sericinus*, *Archon* and others. The body chaetotaxy closely resembles that of *Parnalius* but of not *Sericinus* or *Parnassius*. The extremely long setae are a remarkable characteristic of this genus. (Fig. 6–B, C)

2nd- to last-instar larvae: secondary setae thinner than the primary ones seen on the head and body after the first moult. In the second-instar larva the distinction between the two is easy, but from the second instar onwards the secondary setae increase in number and thickness, making the distinction difficult.

Pupa: firmly supported by a girdle; dark brown in colour and the pupal skin coarse and rugged; the projections on the head not conspicuous; no dorsal protuberances on the thorax or abdomen; the abdomen strongly curved backward due to ventral contraction; provided with a normal cremaster. (Fig. 6–D)

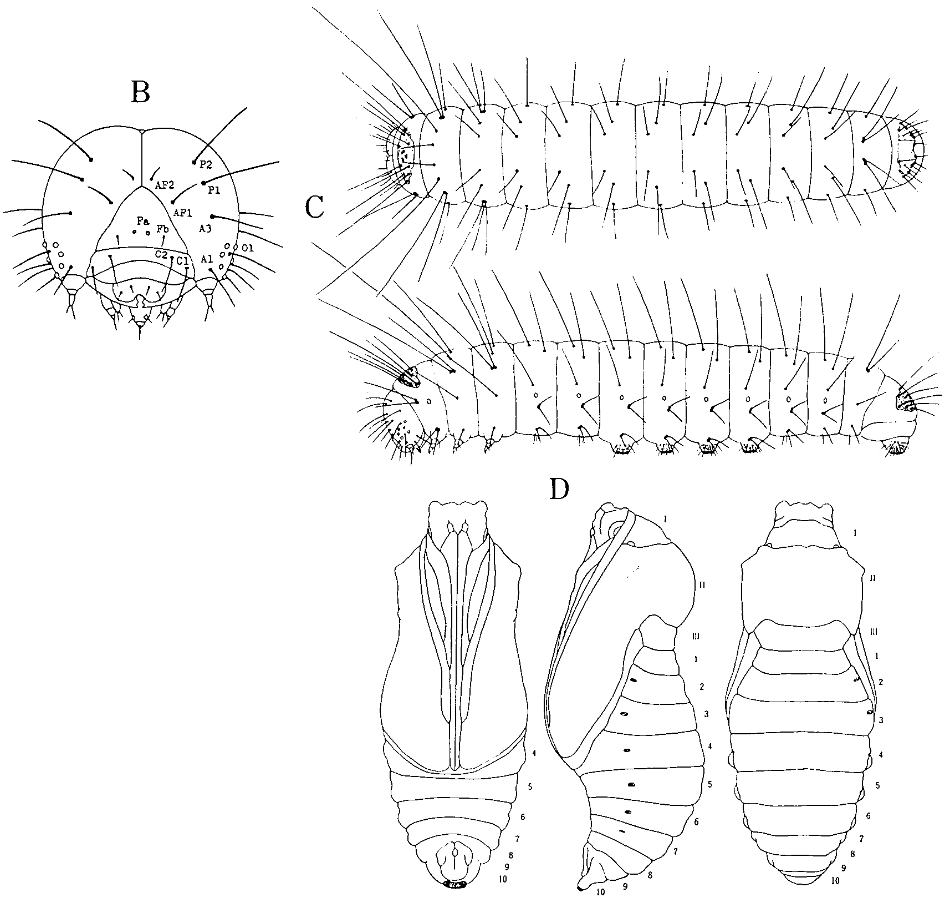


Fig. 6. *Luehdorfia japonica.*

Adult: male genitalia featured by a long, halved uncus, and short hair thickly lining the lower part of the inner side of the valva. The split or forked uncus is a primitive character found only in Zerynthiini and Parnassiini, but the hair on the inner surface of the valva is proper to this genus. After pairing, the female carries a conspicuous sphragis.

Foodplants: Aristolochiaceae (*Asarum*).

Stage of the genus: considered one of the most primitive, along with *Parnalius*, as every aspect of morphology and life history suggests.

Parnalius RASINESQUE 1815

Analyse Nat.: 128, No. 27.

Egg: spherical, pale yellow in colour with pearly lustre.

1st-instar larva: the head chaetotaxy belonging to the basic type; each segment

provided with wart-like subdorsal projections, each carrying a black hair; the osmeterium short and small. (Fig. 7–B, C)

2nd- to last-instar larvae: additional black hairs present on the subdorsal projections, increasing in number as the larva moults; the projections themselves growing longer with the instar; the osmeterium short in all instars.

Pupa: a barbed hook on the vertex catching the transferred girdle. Immediately after pupation, however, the girdle stays just behind the thorax. Later, when the pupal skin has hardened, the pupa vigorously twists its body so as to shift the girdle towards the head. (Fig. 7–D)

Adult: the uncus forked but degenerate; the valve strongly built; no regular sphragis formed after pairing.

Foodplants: Aristolochiaceae, (*Aristolochia*).

Stage of the genus: seen from all aspects of morphology and ecology, this constitutes one of the most primitive genera, along with *Luehdorfia*.

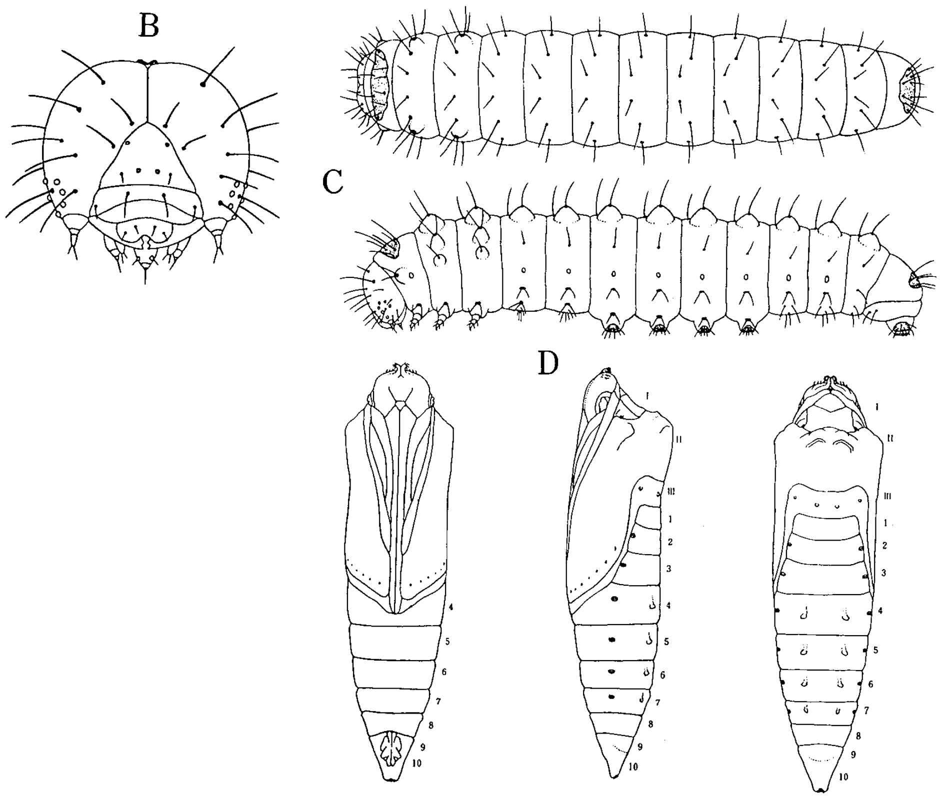


Fig. 7. *Parnalius cerisy*.

Archon Hübner 1822

Syst. -alph. Verz.: 2, 6, 8, 9.

Egg: spherical and smooth-surfaced; green with pearly lustre.

1st-instar larva: head chaetotaxy belonging to the basic type; the body chaetotaxy very similar to that of *Parnassius*, but the number of setae smaller; one point carrying up to two setae; the body colour fairly bright green as against the

dark brown or black body of *Parnassius*; the osmeterium is absent in this instar. (Fig. 8–B, C)

2nd- to last-instar larvae: similar to *Parnassius* in appearance; one white straight hair, much longer than the secondary setae found on either of the subdorsal and subspiracular lines of each segment; the osmeterium is small.

Pupa: not unlike *Parnassius* in appearance but the pupal skin much coarser; the cremaster degenerate.

Adult: the wing venation similar to that of *Parnassius* except for the existence of vein 9. There is no sphragis recognizable.

Foodplants: Aristolochiaceae (*Aristolochia*).

Stage of the genus: both the younger stages and adult characteristics are similar to those of *Parnassius* but considered to be more primitive. That the larval foodplant is *Aristolochia* is indicative of a primitive stage before the specialization of *Parnassius*.

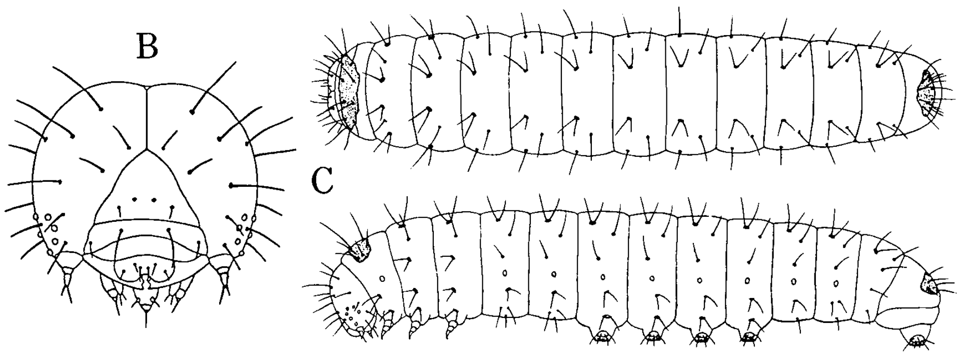


Fig. 8. *Archon apollinus*.

Hypermnestra MÉNÉTRIÈS 1848

Descr. Ins. rec. feu Lehmann: explic. pl. 6, fig. 1.

Egg: spherical and smooth; pure white in colour.

1st-instar larva: the setae on the head found degenerate but the distribution and number of the vestigial points suggestive of the most primitive type; very short hairs found in the lower half of the head.

The setae on the prothoracic plate are mostly reduced to small points, and only very short hairs remain in small numbers. The body chaetotaxy resembles that of *Parnassius* but the setae are largely degenerated and only short ones occur below the basal line. The small point revealing evidence of lost setae does not appear to have accommodated more than two setae. The total number of setae is as small as in *Luehdorfia*. (Fig. 9–B, C)

2nd- to last-instar larvae: the 4th-instar larva with wen-like protuberances on the vertex and adfrons; in the 5th-instar, the vertical protuberances becoming a pair of sharp-pointed horns and the adfrontal ones, a pair of blade-like projections. These cranial protuberances are unknown in the other papilionid species examined. The head and body are studded with points having short hairs.

Pupa: in general appearance similar to *Parnassius*; the cremaster is degenerate. (Fig. 9–D)

Adult: vein 9 absent from the forewing; the antennae short, with flat rounded extremities; the male uncus bifid, and the valva smallish; no sphragis recognized in the female.

Foodplants: Zygophyllaceae (*Zygophyllum*).

Stage of the genus: related to *Archon*, but more specialized both in morphology and choice of hostplants.

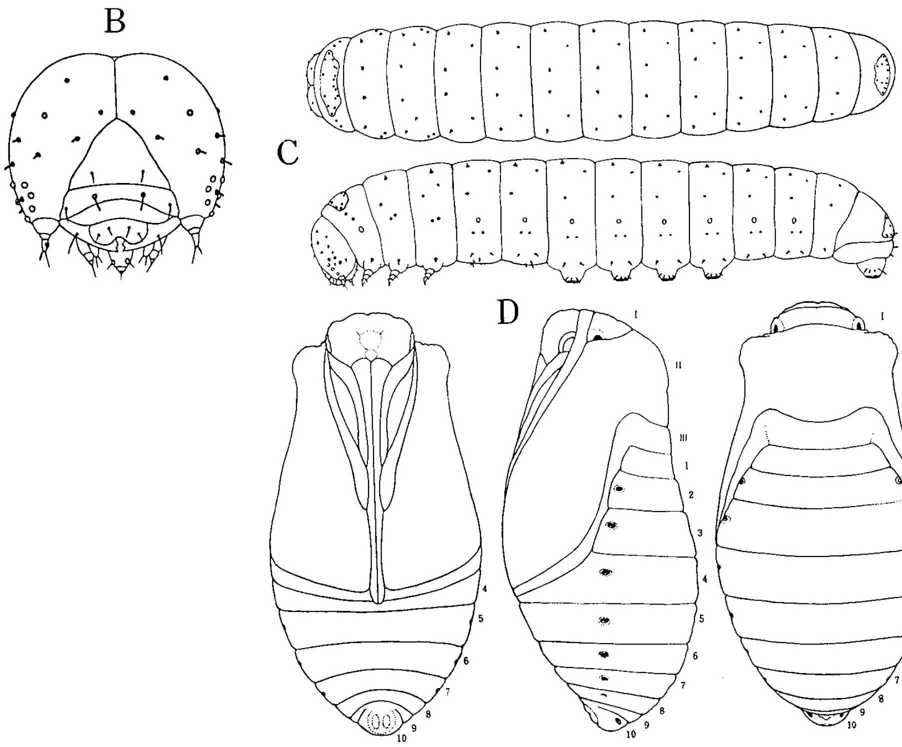


Fig. 9. *Hypermnestra helios*.

Parnassius LATREILLE 1804

Nouv. Dict. Hist. nat. 24 (Tab.): 185, 199.

Egg: flat and whitish without lustre; numerous minute dents seen on the chorion.

1st-instar larva: head chaetotaxy belonging to the basic type, both in the number of setae and their distribution; the distribution of the body setae in agreement with that of *Archon* but their number greater with three to five normal setae growing from one point; the osmeterium absent in this instar. (Fig. 10–B, C)

2nd- to last-instar larvae: short black hairs found on the whole body, but the thicker primary setae easily distinguishable; the osmeterium short.

Pupa: brownish and smooth-surfaced bullet form, with no projections whatsoever. The pupa is in a cocoon and the larval skin is not cast off completely — hence there is no cremaster. (Fig. 10–D)

Adult: lacking vein 9 on the forewing. The uncus is bifid. There is a distinct

sphragis carried by the female.

Foodplants: Papaveraceae, Crassulaceae, Saxifragaceae.

Stage of the genus: morphologically in close association with *Archon*; probably more specialized than *Archon* as a result of adaptation to arctic or alpine climate.

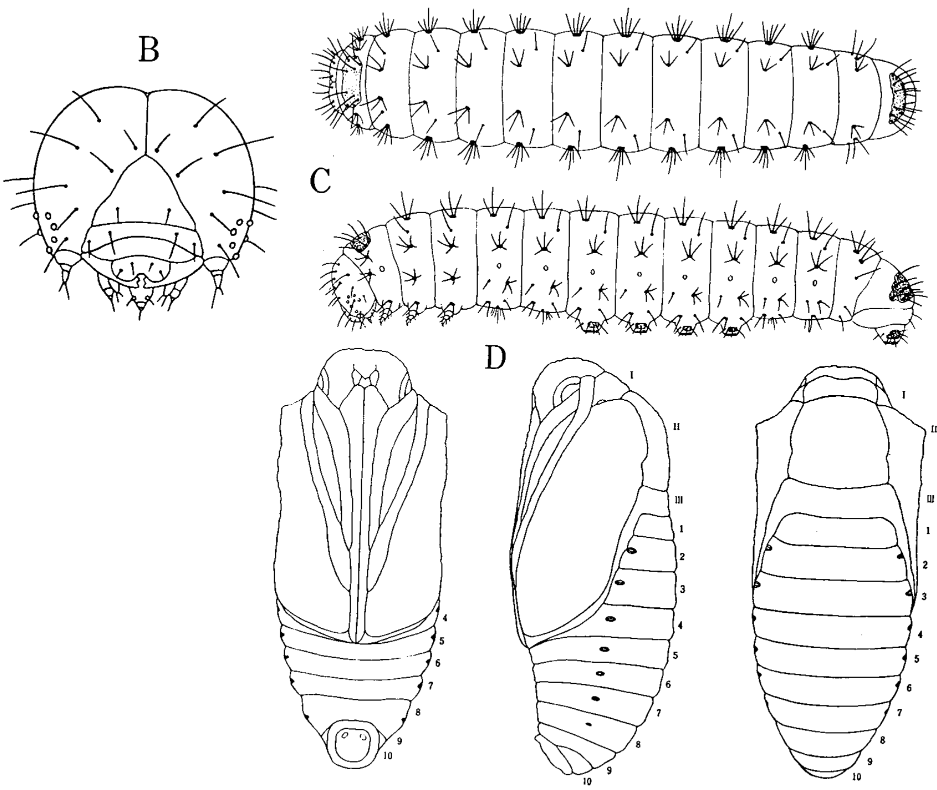


Fig. 10. *Parnassius glacialis*.

Sericinus WESTWOOD 1851

Trans. ent. Soc. Lond. (2) 1, p. 173.

Egg: spherical and pale yellow in colour, similar to *Parnalius*.

1st-instar larva: head chaetotaxy belonging to the basic type and identical with that of *Parnalius* or *Archon*; one subdorsal tubercle found on either side of any of the segments from the mesothorax to the ninth abdominal segment, and one supraspiracular tubercle on each side of any of the thoracic segments; the tip of each tubercle chitinized and carrying six setae. This is a noticeable feature making this genus more complex than *Luehdorfia*, *Parnalius* or *Archon*. (Fig. 11–B, C)

2nd- to last-instar larvae: tubercles developing black hairs besides those on the tips, increasing in number after each moult; the fleshy supraspiracular tubercle on the prothorax longer than the others, becoming longer after every moult; the osmeterium short throughout the instars.

Pupa: not unlike *Parnalius* in general appearance, but the head provided with two

ordinary projections instead of a barbed hook; a pair of small dorsal knobs found on the mesothorax; two sharp-pointed projections on the subdorsal line on either of the fifth and sixth abdominal segments. (Fig. 11–D)

Adult: uncus short, forked but degenerate; the valva not strongly built.

Foodplants: Aristolochiaceae (*Aristolochia*).

Stage of the genus: probably the most advanced of the Zerynthiini, judging from the larval morphology and multi-broodedness.

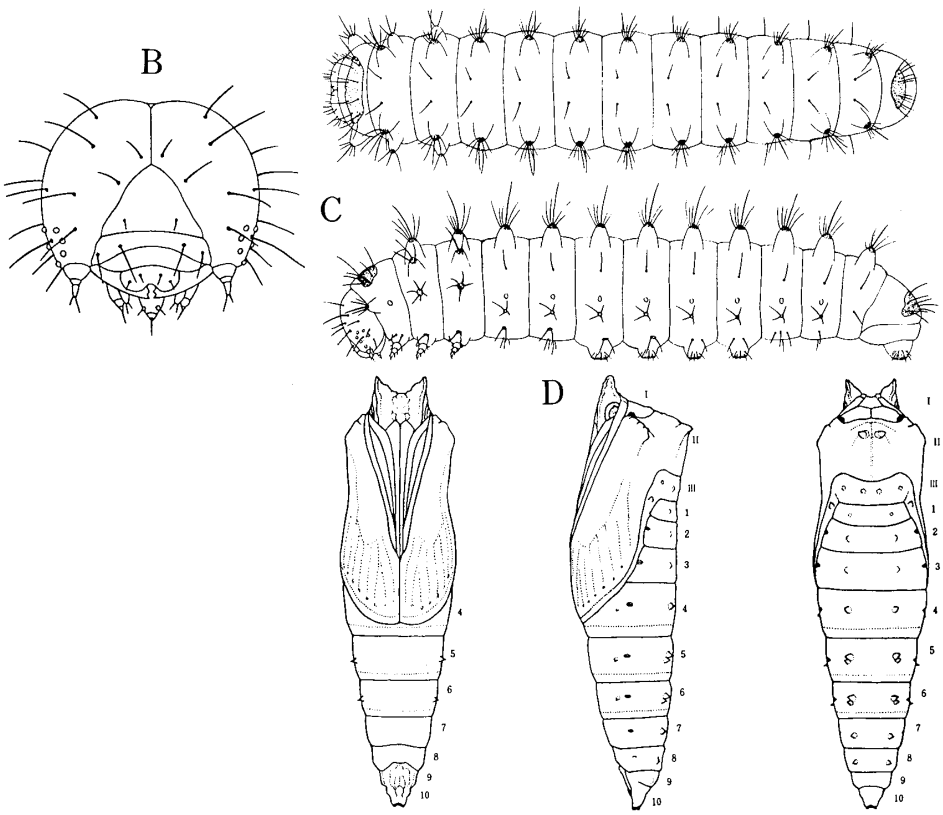


Fig. 11. *Sericinus montela.*

Cressida Swainson 1832

Zool. Illustr. (2) 3 (21): pl. 94.

Egg: spherical and orange in colour; with longitudinal ridges of female secretion converging into a tip on the very top of the chorion.

1st-instar larva: the number and distribution of the setae on the head approximating the most primitive type; the upper part of the head with five small lateral points; each subdorsal tubercle carrying one transparent hair and three black hairs. This number of setae, four, is much smaller than in *Pachliopta* or *Atrophaneura* but a black hair found at the basal part on the rear side of each tubercle is a common feature among these three groups. The spiracles are found in relatively high position, and there are no supraspiracular setae or setae above them while these exist in *Pachliopta* and *Atrophaneura*. Fur-

thermore, there are fewer basal setae. The anal plate is chitinized, but absent in *Pachliopta* or *Atrophaneura*. There are a pair of distinct ventral humps on the second abdominal segment, which are considered to be degenerate prolegs. All these features indicate that *Cressida* is more primitive than *Pachliopta* and *Atrophaneura*. (Fig. 12–B, C)

2nd- to last-instar larvae: morphologically very similar to those of *Pachliopta* and *Atrophaneura*.

Pupa: horny projections on the head, thorax and abdomen much less developed than in *Pachliopta* or *Atrophaneura*; the pupal body almost straight in lateral aspect, as against pupae of *Pachliopta* or *Atrophaneura* which are strongly bent in an S-fashion.

Adult: scales poorly developed in both sexes, leaving part or most of the wings semitransparent; a conspicuous membranous sphragis found in the female.

Foodplants: Aristolochiaceae (*Aristolochia*).

Stage of the genus: so far regarded as an ancestral papilionid, but its early stage morphology suggests more proximity to *Pachliopta*, being more advanced than Zerynthiini or Parnassiini.

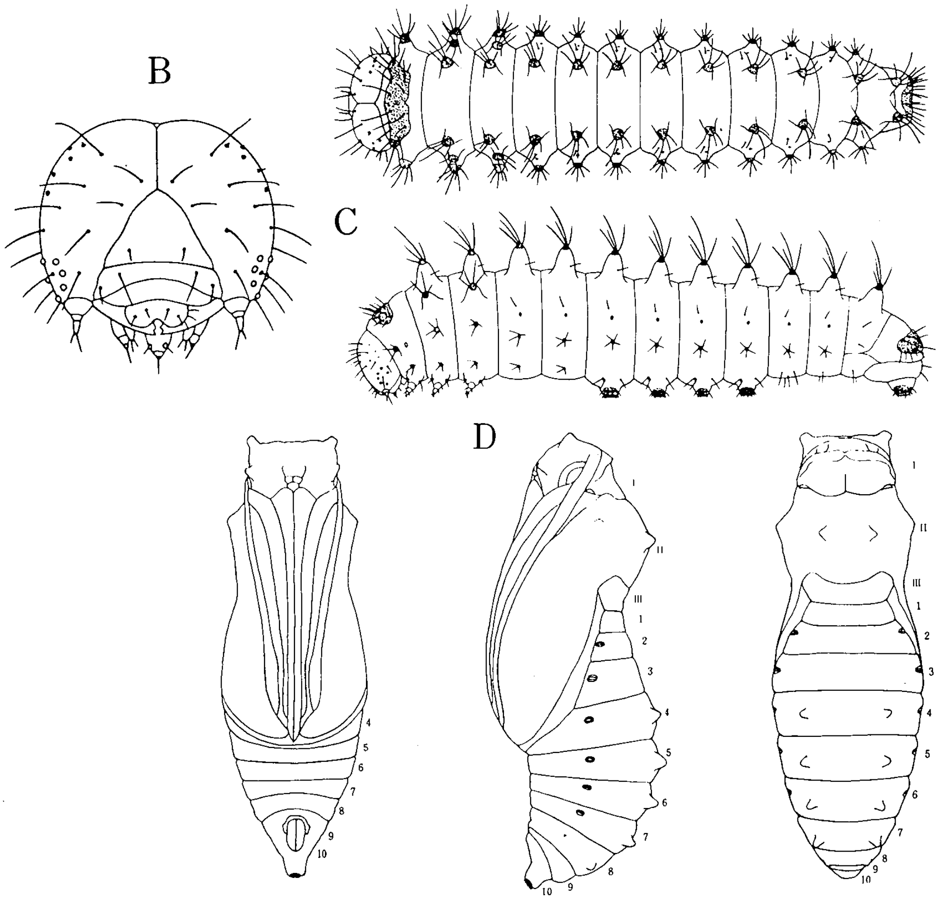


Fig. 12. *Cressida cressida*.

Euryades Felder (C.) & Felder (R.) 1864

Verh. zool. -bot. Ges. Wien 14: 327, 376.

Egg: not examined.

Larvae: not examined; similar to that of *Parides*, according to Burmeister (1878). Probably they have fleshy tubercles similar to those of Oriental *Pachliopta* and *Atrophaneura*.

Pupa: more straight than weakly bent as in *Papilio machaon*, hardly resembling the pupae of *Pachliopta* or *Atrophaneura*. The minute reticular pattern on the pupal skin may suggest its association with *Battus*. (Fig. 13–D)

Adult: sphragis known to exist.

Foodplants: Aristolochiaceae (*Aristolochia*).

State of the genus: about the same as *Cressida* in evolutionary stage but probably more primitive than *Battus*.

D

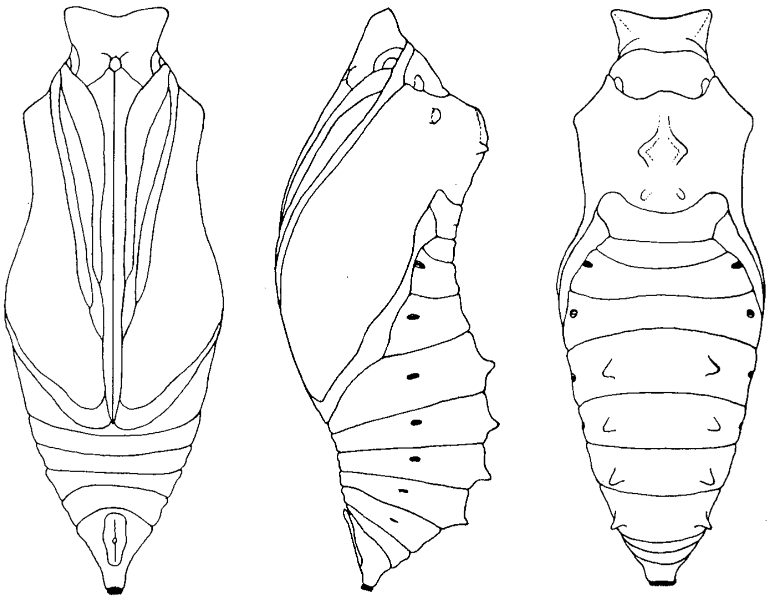


Fig. 13. *Euryades corethrus*.

Pachliopta Reakirt 1865

Proc. ent. Soc. Philad. 3: 503.

Egg: similar to that of *Cressida*; spherical and of grape colour, with longitudinal ridges of orange female secretion; the ridges converging on the top of the chorion to form a point, which is always eccentric.

1st-instar larva: head setae slightly more numerous than the basic types but less than in the allied *Atrophaneura*; the body setae also more numerous than in *Cressida* but less than in *Atrophaneura*. (Fig. 14–B, C)

2nd- to last-instar larvae: exactly similar to those of *Atrophaneura* and no apparent difference recognizable between the two.

Pupa: head with a marginal ridge extending backward; the mesothorax with a thin, lateral lobe on each side and a lambda-shaped protuberance on the dorsal line; the subdorsal protuberances on the 4th to 7th abdominal segments large but thin. (Fig. 14–D)

Adult: male genitalia extraordinarily different from those of *Atrophaneura*.

Foodplants: Aristolochiaceae (*Aristolochia*).

Stage of the genus: higher than *Cressida* but lower than *Atrophaneura*.

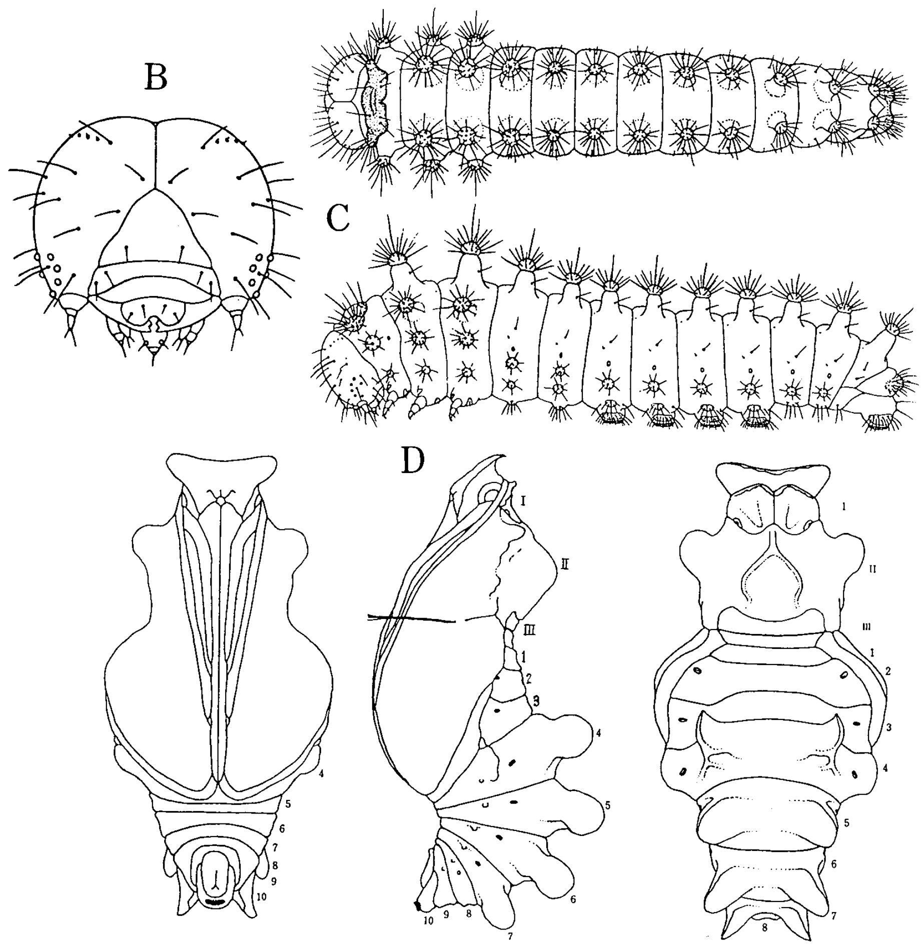


Fig. 14. *Pachliopta aristolochiae*.

Pharmacophagus HAASE 1892

Bibl. zool. 8: 120.

Egg: not examined.

1st-instar larva: not examined.

Last-instar larva: very similar to that of *Atrophaneura*, according to MABILLE, P. (1887).

Pupa: very similar to that of *Atrophaneura*. (Fig. 15–D)

Foodplants: Aristolochiaceae, Combretaceae.

Stage of the genus: closely related to *Pachliopta* but highly specialized, probably due to isolation.

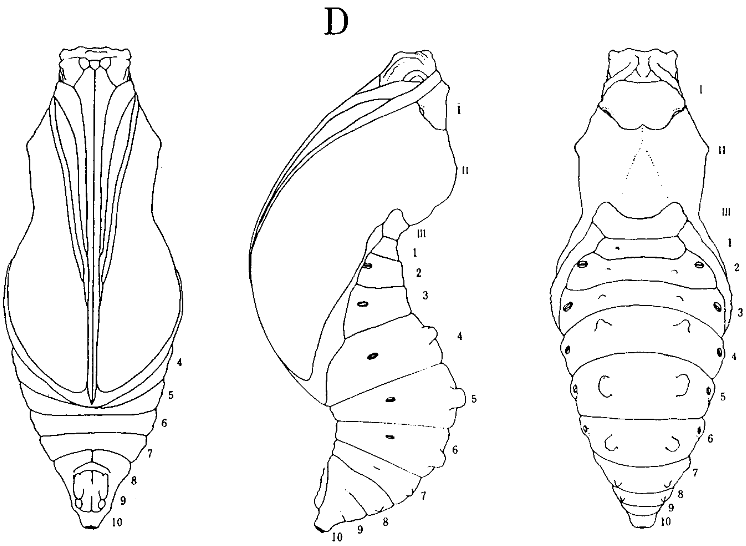


Fig. 15. *Pharmacophagus antenor*.

Battus Scopoli 1777

Introd. Hist. nat.: 433.

Egg: spherical, with longitudinal ridges of orange female secretion, which converge slightly eccentrically into a point on the top of the chorion.

1st-instar larva: not examined.

Last-instar larva: dark purple, with velvety gloss similar to that of *Pachliopta*; the tubercles the same in position as those of *Pachliopta*, whose lengths vary with the species, however.

Pupa: not unlike that of *Pachliopta* but the skin coarser, with short, finely zigzagging lines that look like minute cracks; thorax not bending backward very strongly; head similar to that of *Papilio*; the dorsal protuberance on the mesothorax pronounced as in *Papilio*; the subdorsal rows of flat protuberances rather resembling those seen in *Pachliopta*; a green form known.

Foodplants: Aristolochiaceae (*Aristolochia*).

Stage of the genus: not conclusive, in default of information on the 1st-instar larva; possibly more advanced than *Euryades* or *Cressida* and comparable to *Atrophaneura*.

Troides Hübner 1819

Verz. bekannt. Schmett. (6): 88.

Egg: spherical, smoothly coated with female secretion ranging in colour from red to orange.

1st-instar larva: head chaetotaxy belonging to the basic type, either in the distribution or number of setae; colour of the body dark purplish red; prothoracic plate distinct and chitinized, with its lateral terminal protuberances longer than in *Atrophaneura*. The fleshy tubercles of each segment are in complete agreement in location with those of *Atrophaneura* but rather different in shape, with their setae-carrying sclerotized tips much elongated. There exists a seta at the basal part on the posterior side of the tubercle. As in *Atrophaneura*, the anal plate is not sclerotized and has a very indistinct outline. It carries a pair of low protuberances with black hairs. (Fig. 16–B, C)

2nd- to last-instar larvae: usually of velvety dark wine colour, otherwise grey with a pale orange tint; fleshy tubercles round-tipped in many species but pointed in others; body colour and shape almost unchanged throughout this stage; both the prothoracic and anal plates chitinized and well defined.

Pupa: moderately S-shaped in lateral aspect, but less strongly curved than in *Atrophaneura*; the subdorsal protuberances on and after the 5th abdominal segment blunt in many species but pointed in some others; the body colour either alternating between green and brown, or of a monochrome type of yellow or brown. (Fig. 16–D)

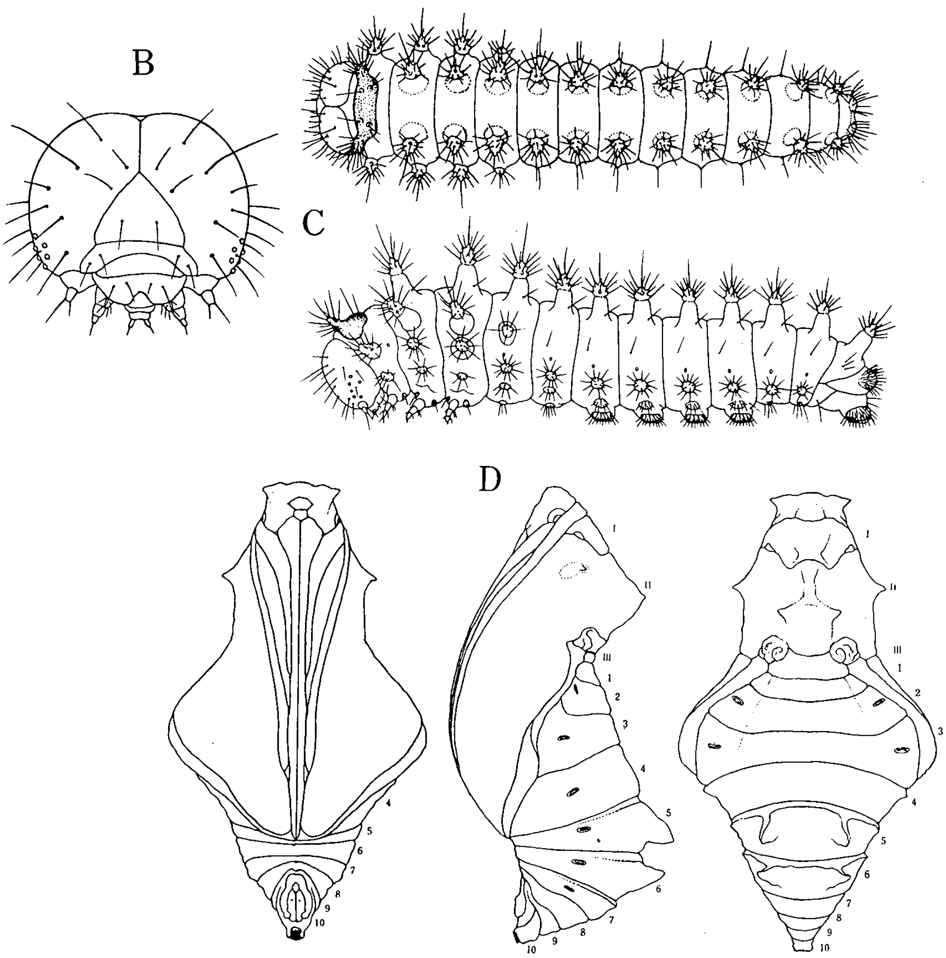


Fig. 16. *Troides aeacus.*

Adult: male forewing long and black, devoid of other colouring than white or grey; hindwing silky golden yellow, margined with black; females with larger and more roundish wings than males, and less intensely coloured. Only females have submarginal spots on the hindwing, which are black.

Foodplants: Aristolochiaceae (*Aristolochia*).

Stage of the genus: early stages and adult morphology suggest an advanced stage of specialization, but probably on a line separate from *Atrophaneura* and lower than that.

Trogonoptera RIPPON 1890

Icon. Ornithopt. 1: 4.

Egg: naturally laid ones not examined.

1st-instar larva: very similar to *Troides*; the sclerotized tips of the subdorsal tubercles not elongated as in *Ornithoptera* but just as long as those of *Troides*.

Last-instar larva: no difference from *Troides* recognizable.

Pupa: no difference from *Troides* recognizable.

Adult: both sexes with metallic emerald green scales which are unknown in *Troides*; brilliant blue spots found on the underside of either sex; the wing form quite distinct from that of *Troides* in that the forewings are elongate and the hindwings are small and roundish; males fond of drinking water, which fact is unknown in *Troides*.

Foodplants: Aristolochiaceae (*Aristolochia*).

Stage of the genus: quite close to *Troides*, except for a few differences including wing venation. These justify the assignment of a separate branch to this genus.

Ornithoptera BOISDUVAL 1832

in D'URVILLE, Voy. "Astrolabe," Faun. ent. 1 (Lép.): 33.

Egg: spherical, with orange or vermillion female secretion forming a smooth, glossy coating.

1st-instar larva: head chaetotaxy identical with that of *Troides*, being the basic type; body colour dark wine red; prothoracic plate chitinized and well defined, with the lateral terminal protuberances longer than in *Troides*; the fleshy tubercles agreeing in position to those in *Troides*, but somewhat different in shape due to their longer chitinized tips; a hair found at the basal part on the rear side of each tubercle; the anal plate not chitinized, carrying a pair of low protuberances on which are found black hairs. (Fig. 17–B, C)

2nd- to last-instar larvae: velvety dark wine red, but grey forms also known; the fleshy tubercles in all species but *victoriae* and unexamined *tithonus* with sharp, chitinized extremities; larvae of different instars similar in colouring and morphology; the prothoracic and anal plates well defined and chitinized.

Pupa: similar to *Troides* except for its slenderer shape, with the lateral extensions of

the 2nd and 3rd abdominal segments less pronounced; also, the subdorsal protuberances on the 4th to 6th abdominal segments smaller and usually more sharp pointed. (Fig. 17–D)

Adult: male forewing mostly black, with bright green and golden yellow areas; hindwing mostly golden yellow, with green spots and black margins; the inner anal margin of the hindwing forming a flap covered with long, white hairy androconiae. Females are generally black with greyish white markings and devoid of green or blue scales.

Foodplants: Aristolochiaceae (*Aristolochia*).

Stage of the genus: somewhat more advanced than *Troides* but still in a lower stage among the papilionids.

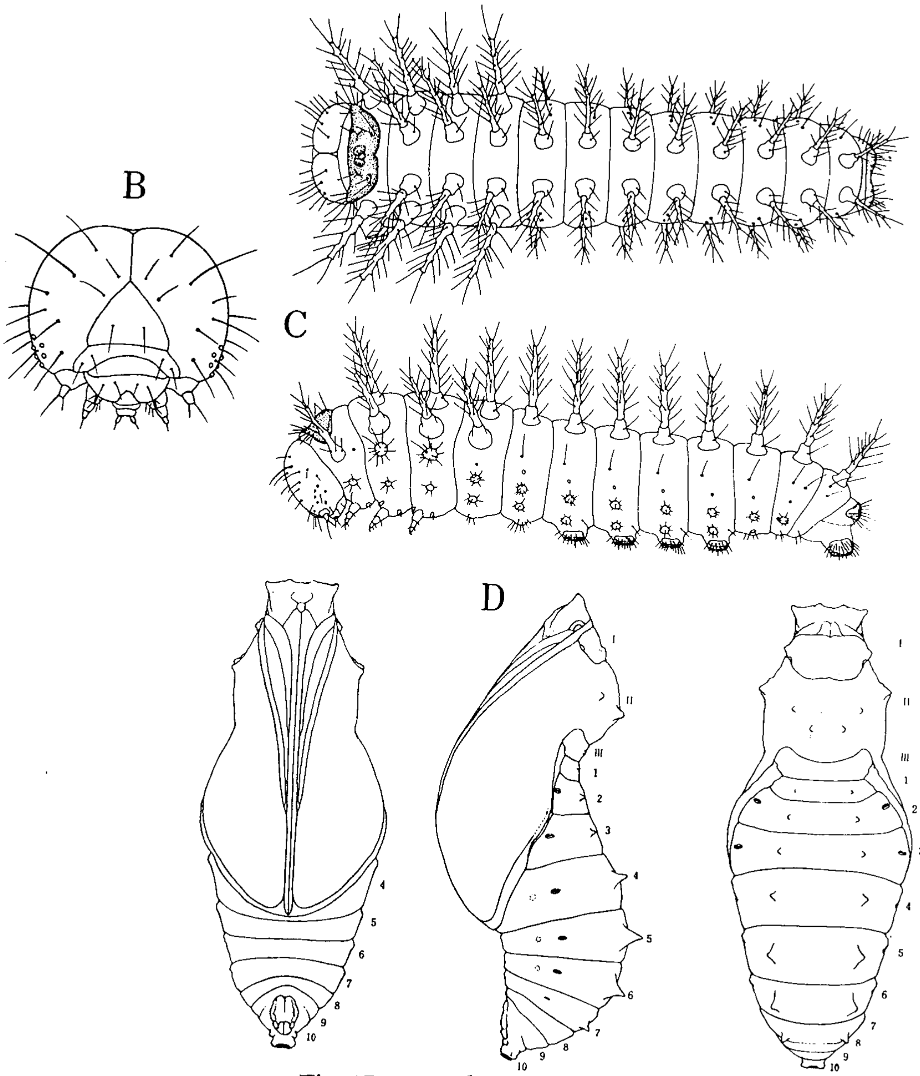


Fig. 17. *Ornithoptera priamus*.

Atrophaneura REAKIRT 1865

Proc. ent. Soc. Philad. 3: 446.

Egg: similar to *Pachliopta.*

1st-instar larva: similar to that of *Pachliopta* except for the remarkably numerous setae on the head. The number and distribution of the setae vary with the species. (Fig. 18–B, C)

2nd- to last-instar larvae: no apparent difference recognizable from those of *Pachliopta*; body colour either dark wine red or greyish.

Pupa: rather strongly bent so that it forms an S-shape in lateral view; mesothorax with a pair of raised, carmine spots; flat, well developed subdorsal protuberances on the 4th and posterior abdominal segments; body yellow or pale brown in colour, and no green forms known. (Fig. 18–D)

Adult: male hindwing with a doubly folded inner anal margin. So far, *Atrophaneura* has been applied to those species without hindwing tails and *Byasa* used for

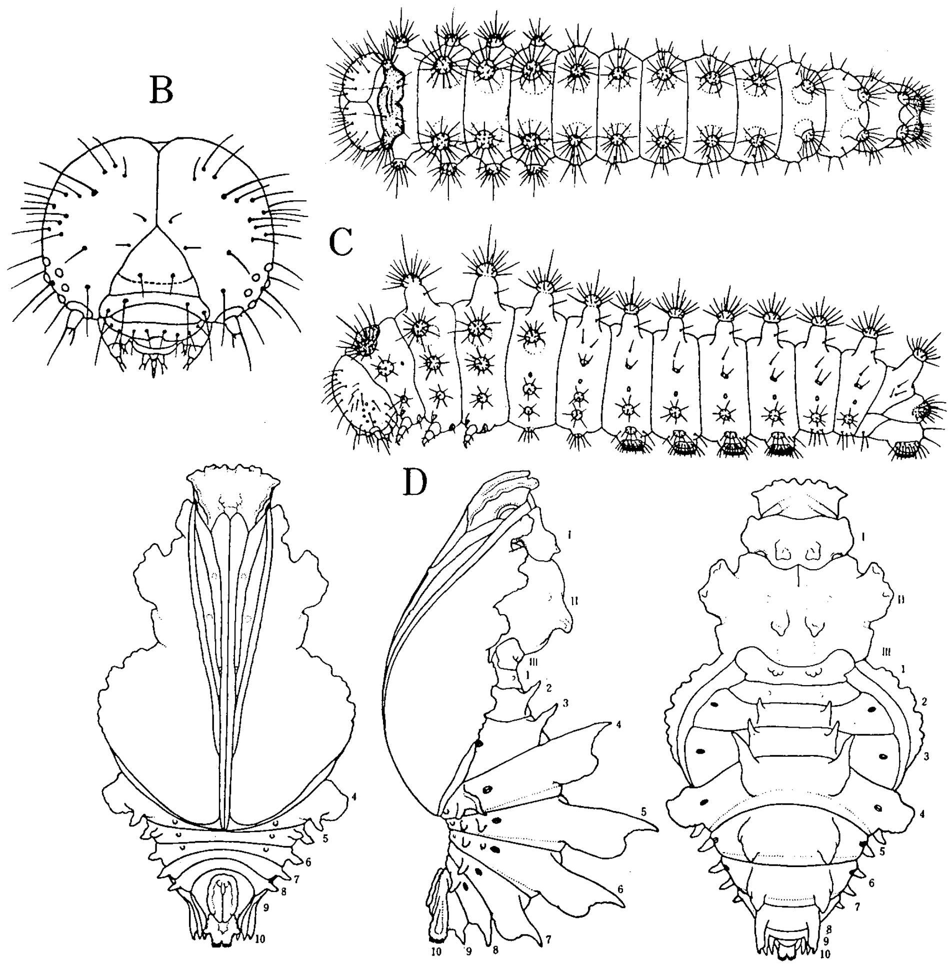


Fig. 18. *Atrophaneura.* B, C: *A. alcinous.* D: *A. nox.*

tailed species, but in all other respects including those of the early stages this distinction has been found superfluous.

Foodplants: Aristolochiaceae, Piperaceae.

Stage of the genus: probably superior to *Pachliopta* because of subtle advanced features found in the early stages.

Chilasa MOORE 1881

Lep. Ceylon 1 (4): 153.

This genus is roughly divided into two: the *epycides* group and the *agestor* group.

1. *epycides* group

Egg: spherical, with granular female secretion attached to the chorion; many laid in a batch.

1st-instar larva: the number and distribution of the setae on the head suggesting a basic type except for a few additional setae; body setae extremely scarce and a point never bearing more than two setae (this pattern is close to that of *Parnalius* or *Luehdorfia* and suggests the relative primitiveness of this genus, which may be in a transitional stage from Zerynthiini to Papilionini); larvae gregarious. (Fig. 19–B, C)

2nd- to last-instar larvae: devoid of conspicuous fleshy tubercles.

Pupa: cylindrical, resembling a broken twig; no green forms known; the ventral surface from the 6th abdominal segment and onwards concave, as if firmly pressed against a twig selected for pupation; the extremity of the pupal midleg on the same level as that of the foreleg. (Fig. 19–D)

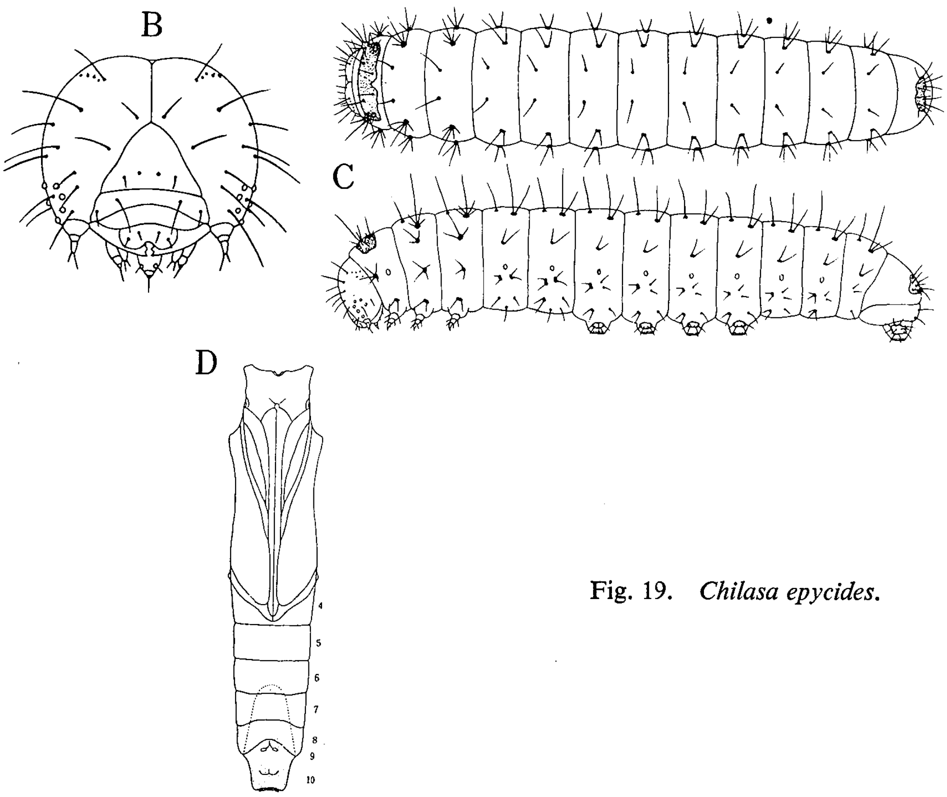


Fig. 19. *Chilasa epycides*.

Species examined: *epycides*.

2. *agestor* group

Egg: spherical, with granular female secretion on the chorion; laid singly.

1st-instar larva: much more complex in some morphological features (for instance, the subdorsal tubercles which assume a cacti-form appearance each carrying several hairs); the larva solitary. (Fig. 20–B, C)

2nd- to last-instar larvae: unlike in *Papilio* or *Menelaides*, the fleshy tubercles becoming longer and larger as the larvae moult and grow.

Pupa: also a broken twig type, but the extremity of the pupal midleg located somewhat posterior to that of the foreleg. (Fig. 20–D)

Species examined: *agestor* and *clytia*; also, *laglaizei*, *toboroi*, *slateri* and *anchisiades*, which may well be included in this group for features such as the cactiform protuberances of the 1st-instar larva and prominent tubercles seen in the older larvae, even though their eggs are laid in batches and the larvae are gregarious — both feautes of *epycides*. *Chilasa anactus* is more similar to *Papilio* in that the egg lacks granular secretions and green pupae are known to occur. Possibly it might be included in a different group.

Adults of both groups: both wings rounded and usually tailless; mostly highly

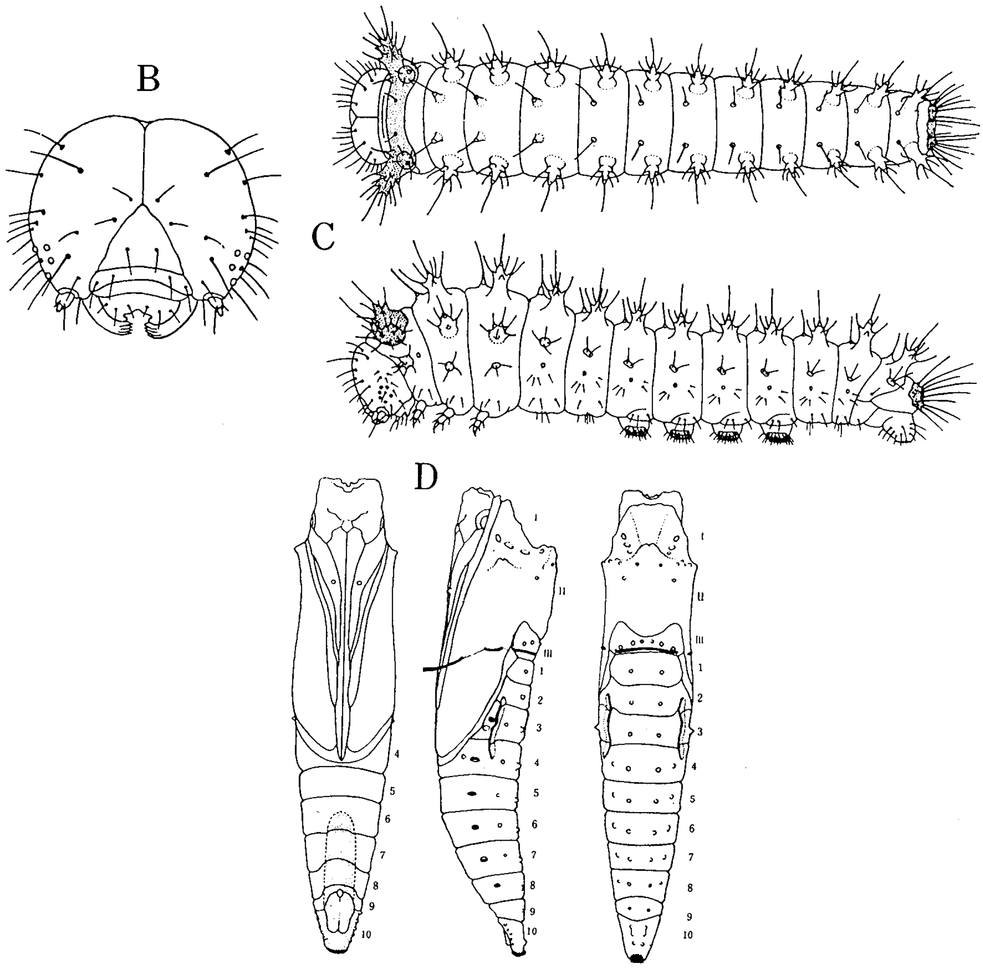


Fig. 20. *Chilasa clytia*.

mimetic, hence few common features recognizable between species. A black and white stripe pattern is seen in many a species but not always. In hindwing venation, this genus is characterized by the shorter distance between veins 5 and 6 on the cell (l_1 in Fig. 21) than between veins 6 and 7 (l_2 in Fig. 21) in many species l_1 is only half as long as l_2. But this is not the case with *paradoxa*, *laglaizei* and *toboroi*. In male genitalia, the harpe is generally large and similar in shape to the valva in these groups.

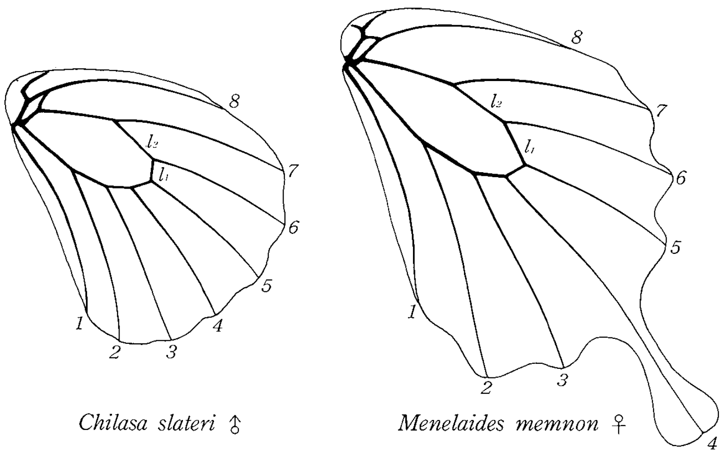


Fig. 21. Hindwing venations in *Chilasa* and *Menelaides*.

Foodplants: Lauraceae, Rutaceae.

Stage of the genus: this genus is rather variable in the stage of evolution, as exemplified by *epycides* having primitive features barely more advanced than those of Zerynthiini, and *clytia* with characteristics approximating those of *Papilio*. Additions to this genus can be expected from among Central and South American papilionids having yellow markings on the forewing, because some of these species are known to have granular secretions on the eggs or *Chilasa*-like male genitalia. These may well prove to be missing links between *Chilasa* and *Papilio*. At least it is safe to say *Chilasa* is immediately below *Papilio*.

Agehana MATSUMURA 1936

Ins. Matsumur. 10 (3): 86.

Egg: exactly the same in shape as that of *Papilio*; no irregular secretion on the chorion; yellow in colour.

1st-instar larva: head setae more numerous than in *Chilasa* but less than in *Papilio* or *Menelaides*, and unique in their distribution. The body morphology including the cactiform tubercles is similar to that of *Papilio* and *Menelaides*.

2nd- to last-instar larvae: generally very similar to those of *Papilio* except that the prothoracic plate is rather widely apart from the posterior margin of the cranium, and that the osmeterium is milky white, a colour which is unknown in *Papilio* but found among the *Chilasa* species.

Pupa: head devoid of conspicuous projections, with the anterior margin forming a rugged but more or less straight line; laterally the head-to-the-mesothoracic-protuberance line forming rather a great angle against the body axis; the latter part of the 7th abdominal segment and onwards ventrally flat and very dark brown in colour (in *Chilasa* the corresponding part is concave and not as dark); the caudal extremity flat and broad in comparison with *Menelaides* or *Papilio*. These characteristics indicate that this genus is very closely related to *Chilasa*. (Fig. 22–D)

Adult: hindwing tail with two veins (this is a unique feature of this genus represented by two species — *maraho* and *elwesi*); male genitalia bearing resemblance to those of *Chilasa*, an indication that this genus would have been derived therefrom.

Foodplants: Lauraceae (*Sassafras* in *A. maraho*) and Magnoliaceae (*Liriodendron* in *A. elwesi*).

Stage of the genus: undoubtedly a derivative of *Chilasa* and probably advanced to the stage of *Menelaides* in view of several morphological features.

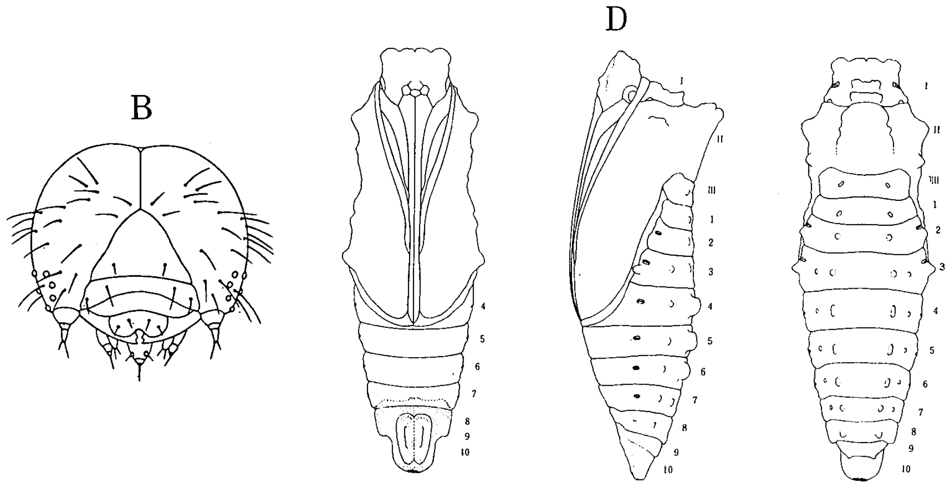


Fig. 22. *Agehana maraho*.

Papilio LINNAEUS 1758

Syst. Nat. (ed. 10) 1: 458.

Egg: high dome-shaped rather than spherical, with a smooth surface.

1st-instar larva: the number and distribution of the setae on the head belonging to the basic type but some secondary setae being present; the pair of protuberances on the prothoracic plate generally short, though there are exceptions; the subdorsal cactiform protuberances shorter than those in *Menelaides* or *Achillides*. (Fig. 23–B)

Last-instar larva: mesothorax and metathorax only moderately thicker than the abdominal segments; the minute hairs on the body straight and not bent backward as in *Menelaides* and *Achillides*. (Fig. 23–C1)

Pupa: head projections not very long and usually wide apart; the mesothoracic dorsal protuberance well developed. (Fig. 23–D)

Foodplants: Rutaceae, Apiaceae.

Stage of the genus: very close to, and slightly more advanced than, *Chilasa*.

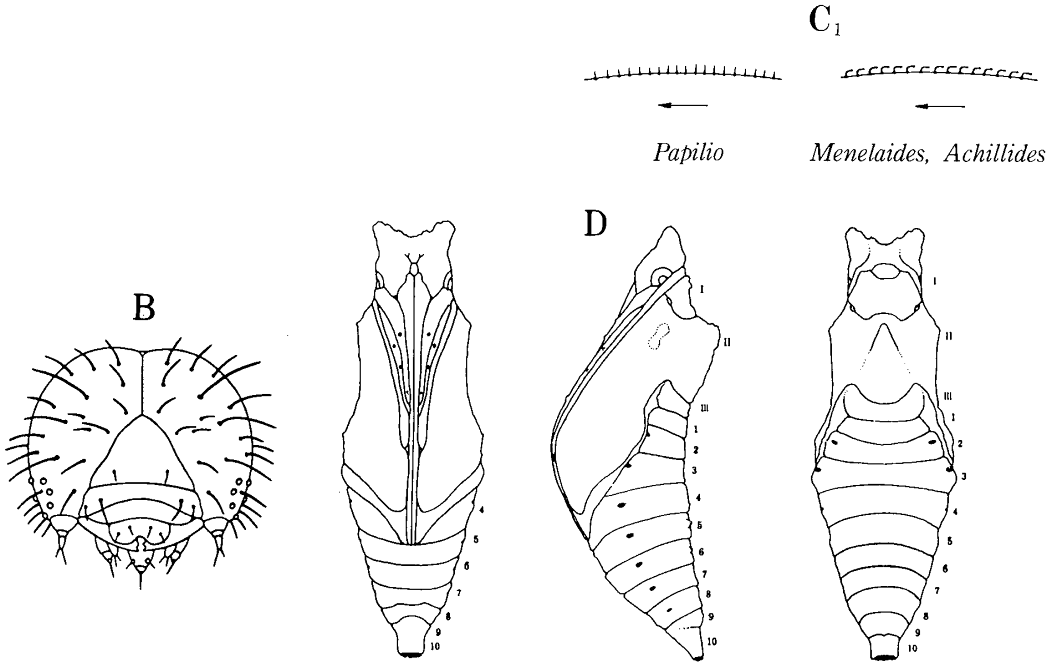


Fig. 23. *Papilio demoleus*.

Euchenor IGARASHI 1979

Papilionidae and their eary stages. 18.

This genus has been established on the basis of a single species *euchenor*.

Egg: almost identical with that of *Menelaides* or *Papilio*.

1st-instar larva: head setae short and more numerous than in *Papilio* but less than in *Menelaides*; the pair of protuberances on the prothoracic plate extremely long and encircled with setae; also, the subdorsal tubercles and the supraspiracular tubercles of the mesothorax and metathorax similarly very long and encircled with setae. While each tubercle is provided with a seta at its very tip in *Papilio*, *Menelaides* and *Achillides*, that of *euchenor* has two lateral setae on its extremity. (P. 49, Fig. 2)

Last-instar larva: a pair of laterally extending protuberances found on the prothoracic plate, and long tubercles also seen on the 5th, 6th and 9th abdominal segments.

Pupa: body bent extremely backward as in some tropical pierids; proboscis very long, with its extremity reaching the anterior margin of the 7th abdominal segment. (Fig. 24–D)

Adult: forewing markings and orange and pale blue spots on the underside of the hindwing not unlike those of *demoleus*, but the male genitalia resembling those of *Chilasa* rather than those of *Papilio*.

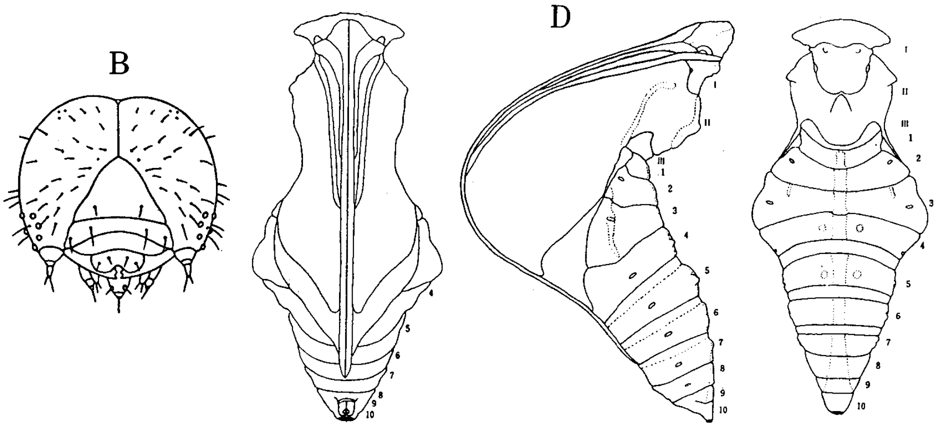


Fig. 24. *Euchenor euchenor*.

Foodplants: Rutaceae.

Stage of the genus: very close to *Papilio* but with morphologically very specialized characteristics.

Menelaides HÜBNER 1816

Verz. bekannt. Schmett. (6): 84.

Once this was erroneously used to denote the genus now called *Pachliopta*; *Menelaides* was originally applied to the species *polytes* (Common Mormon) by HÜBNER in 1816, and is a valid generic name if *polytes* and allied species are separated from *Papilio*. *Menelaides helenus* had a generic name *Charus* MOORE 1881, and *memnon*, *Iliades* HÜBNER 1816. *Charus* is later in date than *Menelaides*, and so is *Iliades*, which was preceded by *Menelaides* though mentioned in the same publication. Thus, *Menelaides* is a valid generic name for both *helenus* and *memnon*.

Egg: high dome-shaped as in *Papilio*, with a smooth surface.

1st-instar larva: head with numerous secondary setae among the primary ones; the pair of protuberances on the prothoracic plate are long and the subdorsal cactiform tubercles well developed. (Fig. 25–B, C)

Last-instar larva: thoracical thickening conspicuous, and the minute hairs on the body bent backward. (P. 80, Fig. 23–C1)

Pupa: head projections long and extending forward; the mesothorax convex but devoid of any prominence. (Fig. 25–D)

Adult: Veins 11 and 12 on the forewing not fused; the inner anal margin moderately folded.

Foodplants: Rutaceae; predominantly *Citrus*, though *Zanthoxylum* and *Evodia* are preferred by some; the *memnon*-group exclusively on *Citrus* and its allies.

Stage of the genus: close to and more advanced than *Papilio*.

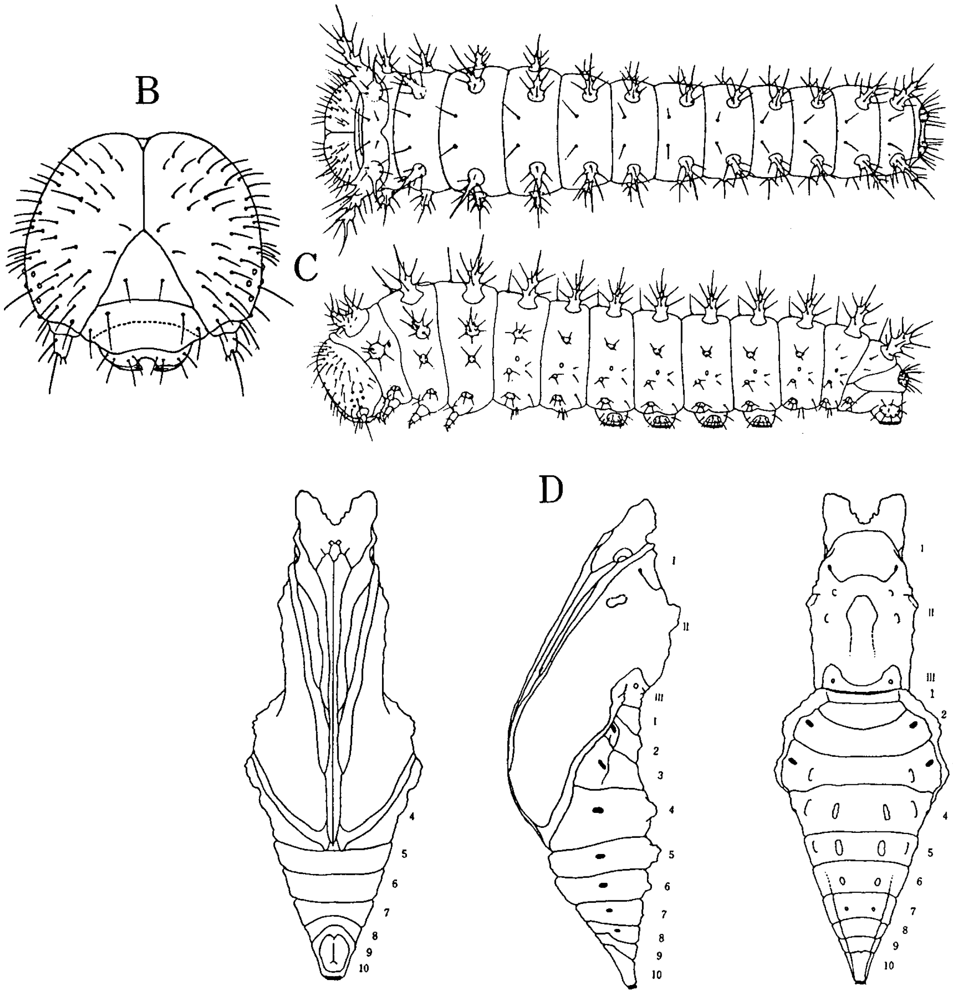


Fig. 25. *Menelaides*. B, C: *M. protenor*. D: *M. bootes*.

Achillides Hübner 1819

Verz. bekannt. Schmett. (6) 85.

Egg: high dome-shaped and smooth-surfaced as in *Papilio*.

1st-instar larva: morphologically almost identical with that of *Menelaides*.

Last-instar larva: a white or pale dorsal arc on the posterior margin of the 1st abdominal segment forming part of an oval line that defines the upper part of the first four body segments, and minute white spots profusely distributed anterior to the arc; the body dotted with minute yellow spots all over.

Pupa: acute subspiracular ridge running from head to end of abdomen on either side; in green pupae the ridges margined with greyish brown. (Fig. 26–D)

Adult: decorated with brilliant blue and/or green scales on the upperside except in *fuscus*, *hipponous*, *canopus* and others.

Foodplants: Rutaceae, but *Citrus* and related species are rarely chosen. In contrast, *Zanthoxylum* and *Evodia* are often preferred.

Stage of the genus: close to *Menelaides*, but the simpler pupal morphology and blue or green scales may entitle them to a more advanced evolutionary stage.

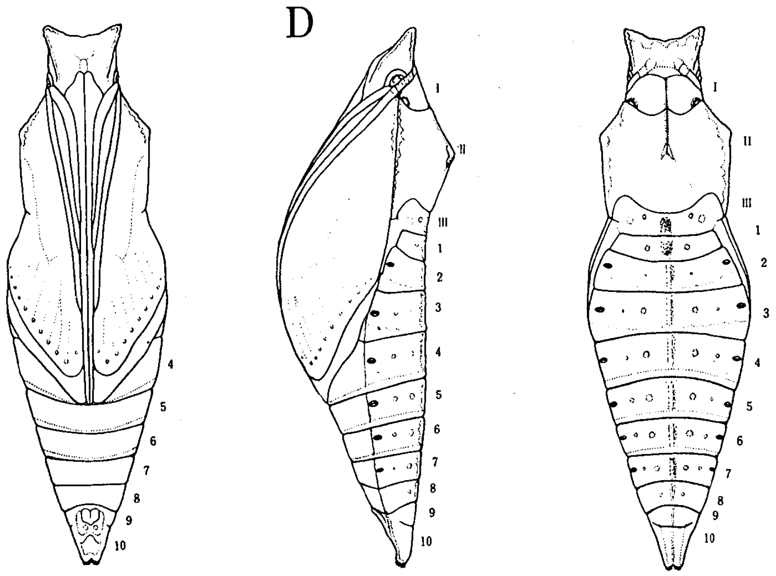


Fig. 26. *Achillides bianor.*

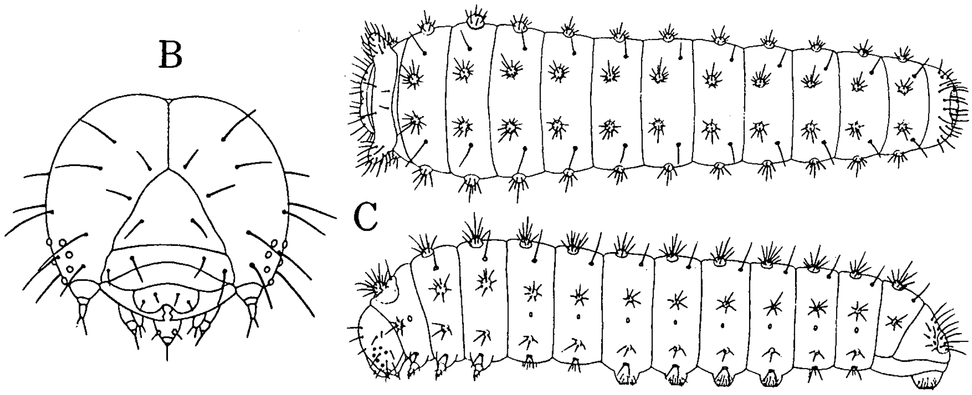
Meandrusa MOORE 1888

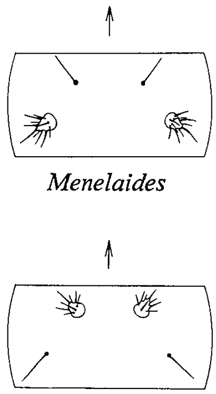
Descr. new ind. Lep. Coll. Atkinson. (3): 284.

Egg: high dome-shaped and pale yellow in colour, thus closer to *Papilio* than to *Graphium*.

1st-instar larva: head chaetotaxy belonging to the basic type, either in the number or distribution of the setae; the prothoracic plate is not sclerotized, and provided with a pair of tubercles; the tubercles hairy but the hairs pointing to all directions and with blunt extremities, unlike in *Papilio*, *Menelaides* or *Achillides*; the dorsal line running between two rows of cactiform tubercles each carrying several setae (in *Papilio*, *Menelaides* and *Achillides* the rows are made up of single normal hairs). There is a subdorsal row of normal setae in *Meandrusa* which point backwards and are located posterior to the tubercles, which are replaced by a row of cactiform tubercles in *Papilio*, *Menelaides* and *Achillides*. In other words, the setae and tubercles take reciprocally different positions between the two groups. (Fig. 27–C1) This pattern of distribution of setae and tubercles is similar to that in *Graphium*. The 10th abdominal segment carries an anal plate, which is absent in *Graphium*; on the other hand, a cactiform tubercle on either side of the anal plate appears to be absent in *Papilio* and related genera. The setae on the body and tubercles are normal straight hairs, and not bifid as in *Graphium* and its allies. The white spots on the 3rd, 4th and 8th abdominal segments are unknown in *Graphium* etc. but are proper to *Papilio*, *Menelaides*, *Achillides* and related groups. (Fig. 27–B, C)

2nd- to 4th-instar larvae: head setae almost degenerated into points but short ones found on the lower half of the head; the prothoracic plate devoid of setae. No trace remains of the 1st-instar setae or protuberances. This feature





C1 Difference between dorsal protuberances in the lst instar larvae: the arrow indicates cephalad

Fig. 27. *Meandrusa payeni.*

distinguishes *Meandrusa* from *Papilio*, *Menelaides* or *Achillides*, but then it is not quite similar to the case of *Graphium*, whose older larvae retain thoracic and caudal projections. The body has oily gloss, which is unknown in *Graphium* but common among *Menelaides* and *Achillides* spp.

Last-instar larva: not examined.

Pupa: not examined.

Adult: though the wing form of *payeni* suggests some relation with *Graphium*, and indeed past authors included *Meandrusa* in Leptocircini, yet it is different from *Graphium* in the following: a) no fusion of veins 11 and 12 seen in the forewing, and b) the inner anal margin of the hindwing is not as completely folded as in *Graphium.*

Foodplants: no natural foodplants have been recorded but a larva managed to live on *Lindera umbellata* (Lauraceae) in captivity. This at least suggests Lauraceae may form part of the natural foodplants.

Stage of the genus: unfortunately the single larva the author had under observation died in the 4th-instar and no information has been available on the mature larva or pupa. This situation makes it very difficult to draw a conclusion on the stage of evolution of this genus but, as far as the larval features of 1st to 4th instars are concerned, *Meandrusa* should be regarded as belonging to Papilionini rather than Leptocircini.

Protographium MUNROE 1961

Canad. Ent. Suppl. 17: 18.

Egg: identical with that of *Graphium*.

1st-instar larva: only photographic information was available, according to which: a) the setae are bifid as in *Graphium*; b) the tubercle on either end of the prothoracic plate is short, and c) the anal plate is chitinized and provided with long hairs, while that in *Graphium* has a pair of long tubercles but is not chitinized. The feature a) suggests that this genus is allied to *Graphium* and b) and c) indicate it is more primitive than that.

2nd- to last-instar larvae: not examined.

Pupa: curiously shaped, with no similar examples found among the related groups; the body short but sharply tapering down towards the tail; the mesothorax with only a vestigial dorsal prominence. (Fig. 28–D)

Foodplants: Annonaceae.

Stage of the genus: unmistakable member of Leptocircini but probably more primitive than *Graphium*.

D

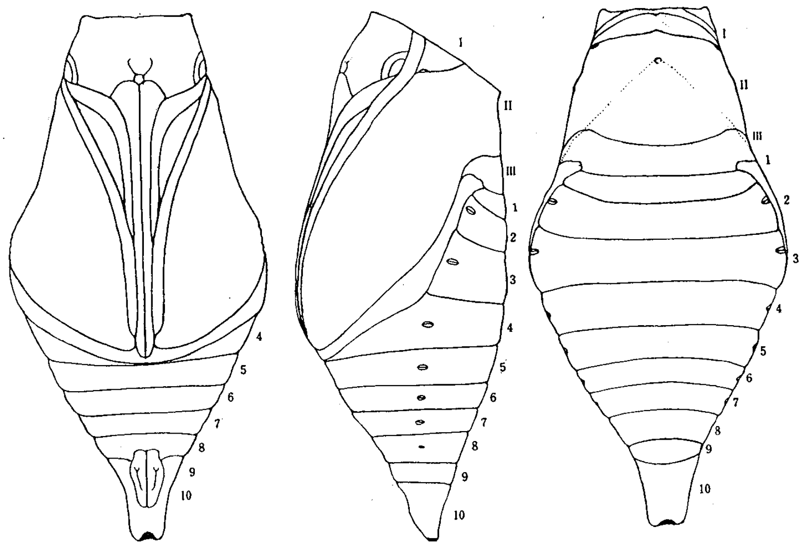


Fig. 28. *Protographium leosthenes*.

Iphiclides HÜBNER 1819

Verz. bekannt. Schmett. (6): 82.

Egg: dome-shaped, and opaque to yellowish white in colour.

1st-instar larva: head setae bifid (only *Baronia* similar in this respect); the setae on the body tubercles also bifid, except those on the 10th abdominal segment; the white dorsal patch on the 3rd to 5th abdominal segment giving a *Papilo*-like impression. (Fig. 29–B, C)

2nd- to last-instar larvae: thorax thickened, body devoid of any tubercles except for a low, wen-like prominence on either edge of the prothoracic plate; the orange spots regularly arranged slightly raised; the osmeterium long.

Pupa: head with a pair of short but sharp protuberances; from a low dorsal protuberance on the mesothorax a total of four raised lines extending, one running dorsally towards the head and, on the opposite side, the dorsal line dividing into two at the anterior margin of the metathorax; and two diagonal, subspiracular lines reaching the tail. These are in complete agreement with those in *Graphium*. The pupal skin is coarser than in *Graphium* and approximates that of *Papilio*. (Fig. 29–D)

Foodplants: Rosaceae.

Stage of the genus: not quite as advanced as *Graphium*, though features of the early stages suggest specialization.

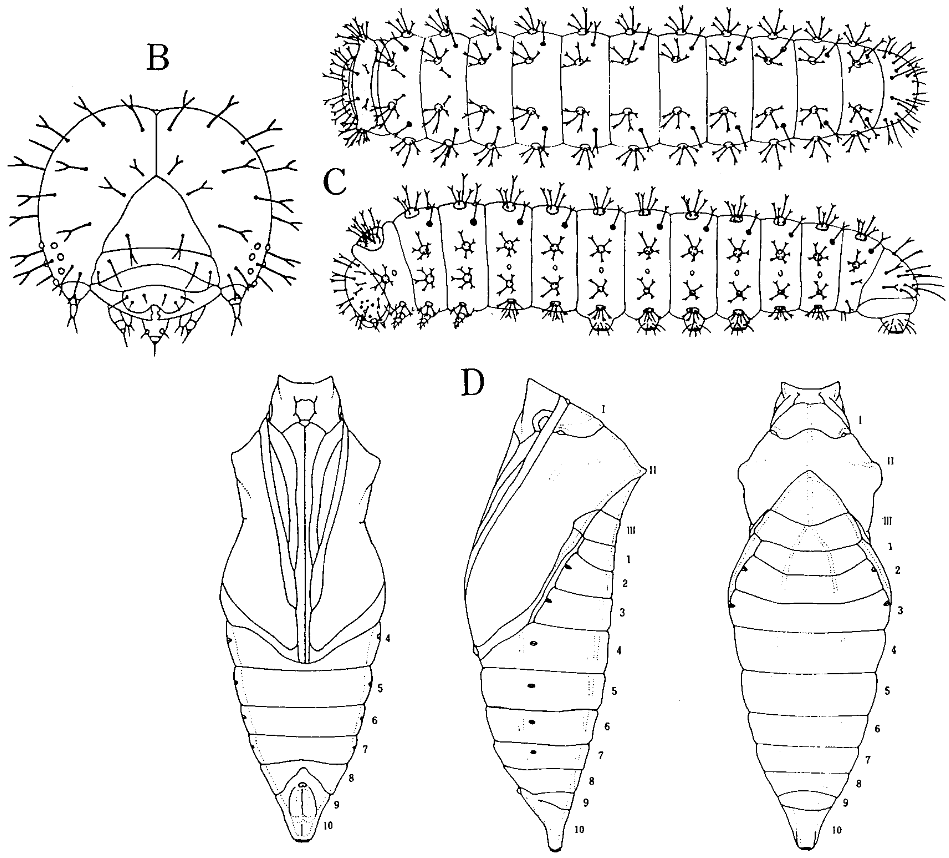


Fig. 29. *Iphiclides podalirius*.

Lamproptera GRAY 1832

in GRIFFITH's Cuvier's Anim. Kingdom 15 (Ins.) pl. 102, fig. 4 (no text).

Egg: high dome-shaped, pale yellow in colour and more glossy than that of *Papilio* or *Menelaides*; similar to a *Graphium* egg in general appearance.

1st instar larva: not examined; similar to that of *Graphium*, according to T. G. HOWARTH (1976). The setae on body points bifid as in *Graphium*.

2nd- to last-instar larvae: more than half of the conspicuous subdorsal tubercles of the 1st-instar larva, namely those on the prothoracic plate, mesothorax, metathorax and the 9th and 10th abdominal segments, disappearing after the first moult; only the foremost and hindmost tubercles continuing to exist, but the others replaced each by a thick primary seta which is distinguishable from a secondary seta; these primary setae lost in the 4th- and 5th-instar larvae; the osmeterium well developed.

Pupa: structurally, if not dimensionally, exactly similar to those of the *sarpedon*-group of *Graphium*.

Adult: forewing partly colourless and transparent; unlike in *Graphium*, veins 11 and 12 are not fused; hindwing tail extremely long.

Foodplants: Hernandiaceae.

Stage of the genus: very close to *Graphium* in respect of early stage characteristics.

Pathysa REAKIRT 1865

Proc. ent. Soc. Philad. 3: 503.

Egg: not examined.

1st-instar larva: not examined.

Last-instar larva: morphologically closely resembling that of *Graphium*.

Pupa: mesothoracic dorsal protuberance very short and found in a more backward position than in *Graphium*. (Fig. 30–D)

Foodplants: Annonaceae.

Stage of the genus: probably related to, but evolutionally at a lower level than, *Graphium*.

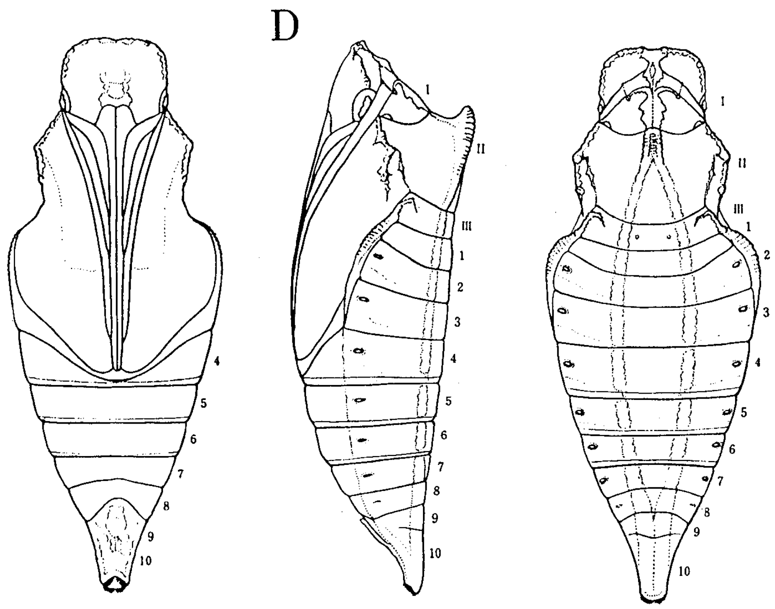


Fig. 30. *Pathysa antiphates*.

Pazala MOORE 1888

Descr. new ind. Lep. Coll. Atkinson. (3): 283.

Egg: spherical and similar to that of *Graphium*.

1st-instar larva: morphologically closely resembling *Graphium*, but the regular pattern of black dots on the body proper to this group.

2nd- to last-instar larvae: tubercles and setae gradually degenerating with the instar unlike in *Graphium*, which loses them except for the thoracic and caudal ones after the first moult.

Pupa: similar to that of *Graphium* but the mesothoracic dorsal horn more strongly protruding forward.

Adult: tails on the hindwing remarkably longer, and the wing patterns more complicated, than in *Graphium*; male genitalia rather different from those of *Graphium*.

Foodplants: Lauraceae.

Stage of the genus: very close to, but slightly more primitive than, *Graphium*.

Graphium SCOPOLI 1777

Introd. Hist. nat.: 433.

Egg: highly spherical, pale yellow in colour; more glossy than in *Papilio* or *Menelaides*.

1st-instar larva: head chaetotaxy belonging to the basic type, both in the number and distribution; the setae on body points bifid, as in *Iphiclides* and *Protographium*; those on the caudal protuberances not bifid. (Fig. 31–B, C)

2nd- to last-instar larvae: all the tubercles lost after the first moult save the subdorsal ones on the three thoracic segments and those on the 10th abdominal segment; the thoracic thickening much pronounced.

Pupa: bullet-shaped, with a prominent dorsal horn on the mesothorax; yellowish ridges running longitudinally, as if simulating leaf veins. (Fig. 31–D)

Adult: veins 11 and 12 on the forewing fused into one, which is a secondary specialization evidencing a high evolutionary stage; this characteristic also found in *Baronia*; the inner anal margin of the hindwing folded, more strongly in males, which have long white hairs in the flap thus formed; the wing membrane partly coloured with blue or green, where scales are absent; in the male genitalia, the uncus very poorly developed.

Foodplants: Lauraceae, Hernandiaceae, Magnoliaceae, Annonaceae, Apocynaceae, etc.

Stage of the genus: evolutionally the most advanced of the known papilionid groups, although some primitive features (*e.g.*, head chaetotaxy in 1st-instar larva) exist.

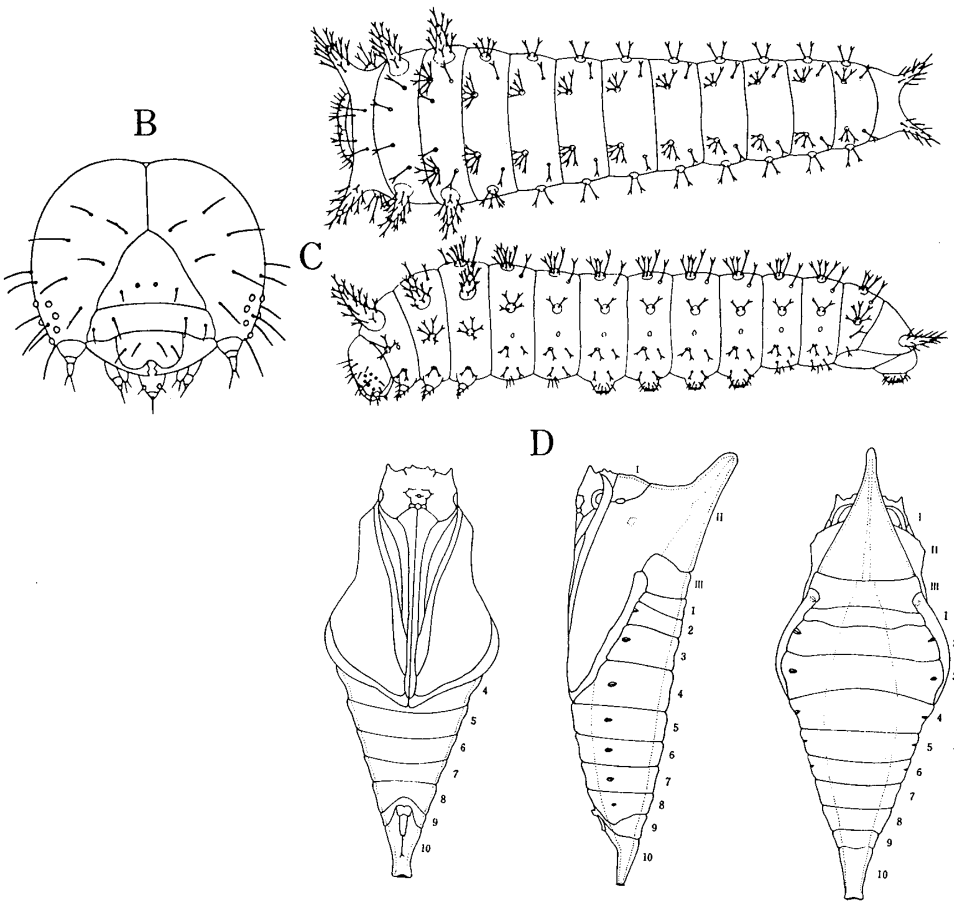


Fig. 31. *Graphium*. B, C: *G. sarpedon*. D: *G. doson*.

Teinopalpus Hope 1843

Trans. Linn. Soc. Lond. 19 (2) 13.

There are accounts of the larva and pupa of this species having been seen in Northern India but, there is neither their detailed description nor illustration, much less photographs. The only information on its early stages concerns eggs extracted from females.

Egg: high dome-shaped, as in *Papilio* and *Menelaides*. However, it has not been known whether naturally laid ova are without noticeable secretion on the chorion.

Adult: sexually dimorphic in wing shape and venation; male with one hindwing tail but two in female; female hindwing extremely broad. Also, flight habits differ between the sexes, with males flying vigorously but females rather awkwardly.

Wing venation is characterized by a rudimentary median spur, which is well developed in almost all other papilionids. Long palpi are found in both sexes.

Foodplants: unknown.

Stage of the genus: rather difficult to determine for want of information on early

stages as well as larval foodplants; adult morphology suggests remote association with Leptocircini.

Phylogenetic Consideration

The author re-examined the particulars of most of the known genera of the Papilionidae by comparing the past theories of classification based on adult morphology with his data on the early stages plus various information on the habits of larvae and adults as well as larval foodplants. The result is summarized in the following points for revision.

1. Denial of the view that *Euryades* and *Cressida* are ancestral forms held by STAUDINGER, SCHATZ and RÖBER (1892) and FORD (1944) in favour of recognition of *Luehdorfia* and *Parnalius* as ancestral Papilionids.

2. Inclusion of the Parnassiinae in the Zerynthiinae from the viewpoint that the Zerynthiini constitutes the main stem in the evolution of the Papilionidae, and that the Parnassiini forms a very specialized branch thereof.

3. Reconfirmation of *Chilasa* as an independent genus following SHIRÔZU (1955), about whose view on *Chilasa* some specialists have been skeptical. In addition, the present author has included *laglaizei*, *toboroi* and *anactus*, whose affiliations have so far admitted of various possibilities, in this genus. Also, he recognized *anchisiades*, a South American species, as the first representative of this genus in this region.

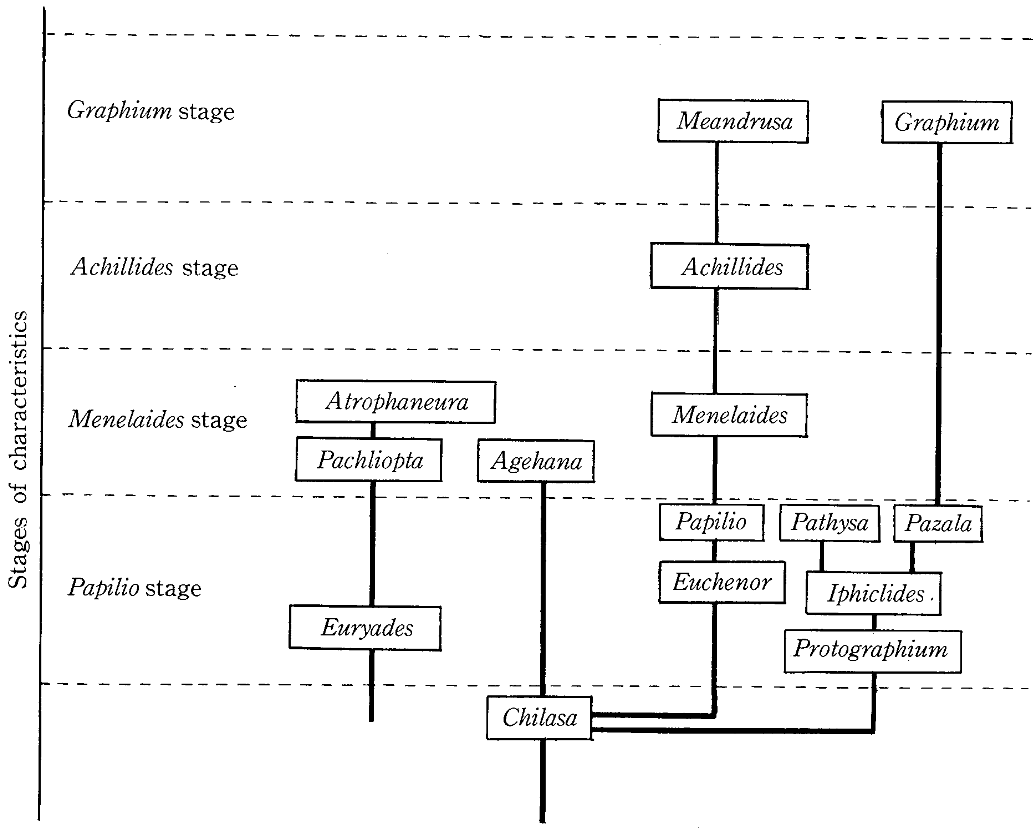


Fig. 32. Parallel evolution in the Papilionidae.

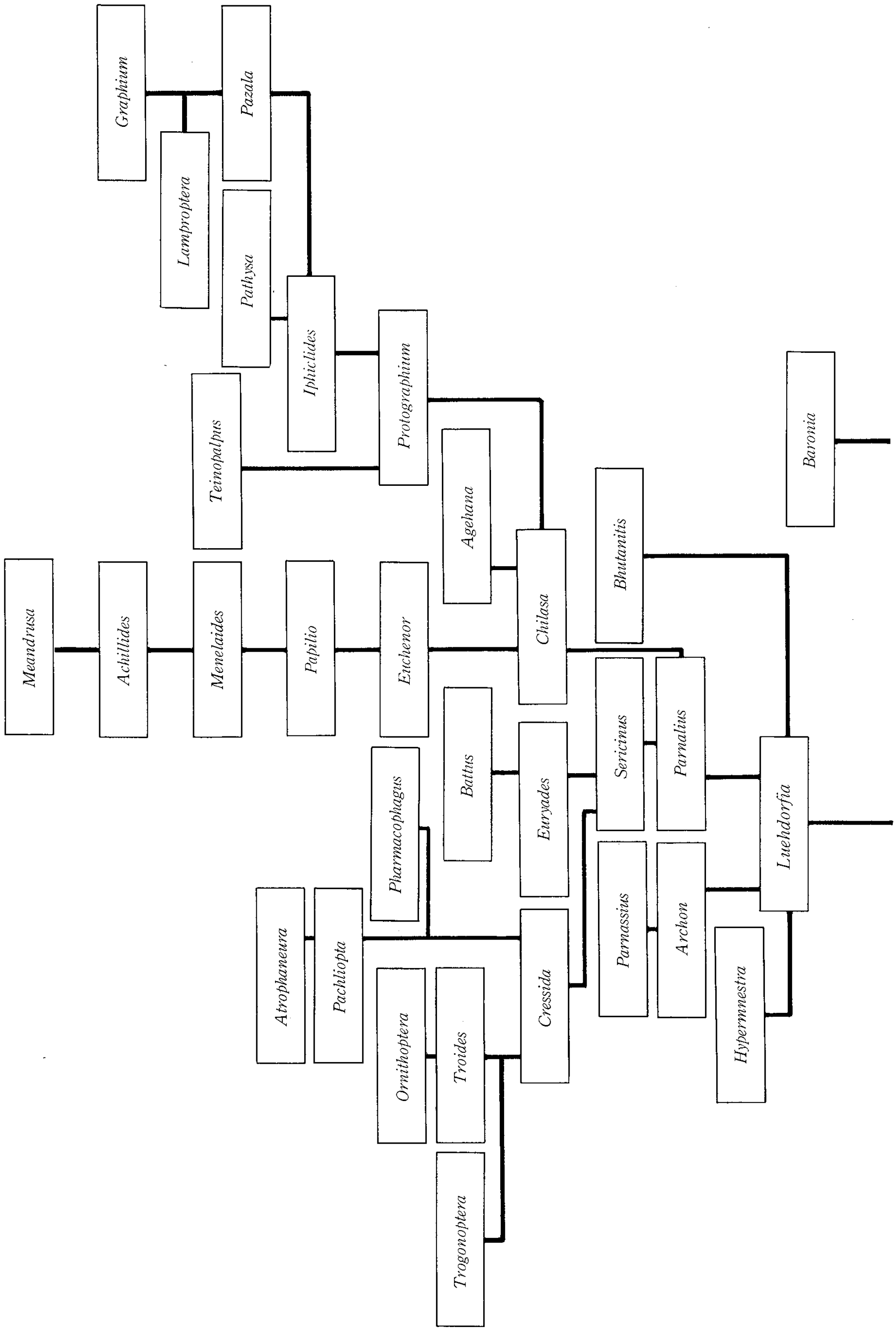


Fig. 33. Intergeneric phylogenetic relationship in the Papilionidae.

4. Recognition of *Euchenor* as an independent genus represented by the species *euchenor*.

5. Division of the traditional "True *Papilio*" into four genera, *Papilio*, *Menelaides*, *Euchenor* and *Achillides*, by reason of apparent differences in early stages and adult characteristics. In the author's opinion, the "True *Papilio*" has long remained an unduly comprehensive group despite its remarkable diversity.

6. Transfer of *Meandrusa* from the Leptocircini, to which it has provisionally been affiliated, to the Papilionini by reason of newly-obtained in formation on early stages.

7. Assignment of *Bhutanitis*, *Teinopalpus* and *Drurya* to provisional positions in the phylogenetical trees on the basis of known morphological information on genitalia and venation, pending the elucidation of their early stages.

When comparing a number of papilionid butterflies, a specialist often finds it difficult to distinguish among species which are similar in appearance but in reality belong to different lines of descent.

For instance, *Atrophaneura*- and *Pachliopta*-species look similar to very remote *Menelaides* species; *Euryades*, to some species of the *Papilio machaon*-group; *Agehana*, allied to *Chilasa*, resembles *Menelaides* in appearance; *Meandrusa*, a derivative of *Menelaides*, shares many aspects with *Graphium* such as morphology, foodplants and habits.

Also to be noted are the similarities found among the characteristics of some species or groups of species that have evolved in areas widely separated from one another. A good example is the North American species *Papilio troilus* vis-à-vis *Achillides* of Asia. Not only does it have turquoise scales on the wing, but its larva and pupa bear resemblance to those of the latter; there must be something more than a mere coincidence here. The larva and pupa of *Papilio nireus* of southern Africa, having blue scales, are known to have characteristics similar to those of *Achillides*.

It appears necessary to recognize a principle to account for these phenomena, which cannot be adequately explained by evolution along a single line of the phylogenetic tree. Thus the author proposes: "Exterior characteristics of papilionids acquired during evolution will ultimately converge on identities, no matiter by what line they are descended."

It may be added that many common characteristics also appear in the course of evolution. This tendency, along with other causes, probably works for the establishment of mimetic characteristics. The author has therefore proposed the term "stages of characteristics" to denote the category of common features found in different groups of papilionids. The ranges are indicated in a preceding diagram (p. 90, Fig. 32). Although it is difficult to apply this idea to such primitive groups as *Luehdorfia*, *Parnalius* and *Archon*, it appears sound to analyze by it the phylogeny of more advanced — or newer — groups.

The Species in the Genera Mentioned

1) Representative species of the 30 genera introduced in this work are given.
2) Genera of the species whose early stages are unknown have been excluded (*e.g. Bhutanitis*, *Druryia*).

3) Known genera may not be represented by species whose former classification under them admits of doubt.

Baronia *brevicornis*
Luehdorfia *japonica, puziloi, chinensis*
Parnalius *polyxena, rumina, cerisy*
Hypermnestra *helios*
Archon *apollinus*
Sericinus *montela*
Parnassius *glacialis, stubbendorfii, mnemosyne, eversmanni, nordmanni, clarius, clodius, orleans, apollonius, honrathi, bremeri, phoebus, actius, jacquemontii, epaphus, tianschanicus, nomion, apollo, hardwickei, szechenyii, cephalus, pythia, acco, przewalskii, rothschildianus, hannyngtoni, maharaja, patricius, acdestis, delphius, stoliczkanus, stenosemus, imperator, charltonius, autocrator, inopinatus, loxias, simo, tenedius, smintheus*
Cressida *cressida*
Euryades *corethrus, duponchelii*
Battus *philenor, devilliersi, zetes, streckerianus, archidamas, polydamas, philetas, madyes, polystictus, belus, eracon, laodamas, lycidas, crassus*
Pachliopta *aristolochiae, polydorus, polyphontes, jophon, pandiyana, oreon, liris, strandi, mariae, phegenus, schadenbergi, atropos, coon, neptunus, rhodifer, hector*
Atrophaneura *semperi, horishana, aidoneus, varuna, zaleucus, nox, luchti, hageni, sycorax, priapus, dixoni, kuehni, sauteri, alcinous, febanus, plutonius, impediens, mencius, laos, nevilli, adamsoni, daemonius, crassipes, polyeuctes, dasarada, latreillei, polla*
Pharmacophagus *antenor*
Troides *aeacus, rhadamantus, magellanus, minos, helena, oblongomaculatus, prattorum, hariphron, criton, vandepolli, darsius, riedeli, amphrysus, cuneifera, miranda, andromache, hypolitus*
Trogonoptera *brookiana*
Ornithoptera *priamus, croesus, aesacus, paradisea, meridionalis, goliath, tithonus, chimaera, victoriae, alexandrae, rothschildi*
Chilasa *epycides, slateri, paradoxa, clytia, agestor, toboroi, laglaizei, moerneri, veiovis, anactus, anchisiades, hyppason, pelaus, oxynius, epenetus, pharnaces, erostratus, erostratinus, rogeri, maroni, isidorus, rhodostictus*
Agehana *maraho, elwesi*
Papilio *machaon, hospiton, alexanor, zelicaon, bairdii, rudkini, nitra, polyxenes, indra, brevicauda, xuthus, demoleus, demodocus, grosesmithi, erithonioides, menestheus, lormieri, ophidicephalus, demolion, liomedon, noblei, antonio, gigon, andraemon, machaonides, cresphontes, ornythion, lycophron, thersites, androgenus, aristor, caiguanabus, aristodemus, paeon, homothoas, thoas, glaucus, rutulus, multicaudatus, eurymedon, alexiares*
Euchenor *euchenor*
Menelaides *protenor, macilentus, alcmenor, bootes, thaiwanus, mayo, memnon, poly-*

mnestor, ascalaphus, rumanzovia, deiphobus, lampsacus, forbesi, acheron, oenomaus, jordani, helenus, sataspes, iswara, iswaroides, diophantus, polytes, ambrax, phestus, aegeus, tydeus, bridgei, weymeri, gambrisius, inopinatus, oberon, heringi, woodfordi, godeffroyi, schmertzi, amynthor, ptolychus, erskinei, albinus, nephelus, castor, mahadeva, dravidarum.

Achillides *fuscus, hipponous, canopus, bianor, polyctor, chikae, maackii, dialis, elphenor, krishna, arcturus, hoppo, paris, karna, crino, palinurus, buddha, blumei, peranthus, pericles, lorquinianus, neumoegeni, ulysses, montrouzieri, nireus*

Pterourus *troilus*

Meandrusa *payeni, gyas*

Teinopalpus *imperialis, aureus*

Protographium *leosthenes*

Iphiclides *podalirius*

Lamproptera *meges, curius*

Pathysa *antiphates, agetes, stratiotes, nomius, aristeus, rhesus, dorcus, androcles, euphrates, epaminondas*

Pazala *eurous, alebion, glycerion, tamerlanus, phidias*

Graphium *sarpedon, milon, cloanthus, weiskei, stressmanni, gelon, codrus, empedovana, mendana, doson, eurypylus, evemon, bathycles, leechi, arycles, agamemnon, meeki, macfarlanei, meyeri, procles, wallacei, hicateon, browni, morania, leonides, policenes*

Acknowledgements

The author's thanks are due to the late Mr. Tarô IWASE, former President of the Lepidopterological Society of Japan, Dr. Takashi SHIRÔZU, present LSJ President, Dr. Syôzirô ASAHINA, Dr. Yoshihiko KUROSAWA, Dr. Shun-Ichi UÉNO, Mr. T. G. HOWARTH, Dr. Atuhiro SIBATANI, Dr. Masami OGATA, Dr. Kôhei SAKAGUTI, Dr. Rokurô KANÔ, Mr. Toyohei SAIGUSA, Mr. Kazuhiko MORISHITA, Mr. Haruo KIMURA, Mr. Yoshiaki OHNO and others, for their academic advice and suggestions. Valuable information and living materials were supplied to the author by Mr. C. G. C. DICKSON, Mr. Yukio TABUCHI, Mr. Hiroshi ONO, the late Mr. Isamu HIURA, Mr. Kaiya KUBO, Mr. Tadahiro TAKAKURA, Mr. Haruo FUKUDA, Sra. Leonila VÁZQUEZ, Sr. Hector PÉREZO R., Mr. Nada SANKOWSKY, Mr. J. -P. VESCO and others. The author greatly benefited from company and co-operation in his overseas activities of Dr. Yoshirô KUDÔ, Mr. Motohiro HARADA, Mr. Yasushi KONII, Mr. Tadashi ISHII, Mr. Yoshiaki GUNJI and Mr. R. STRAATMAN both in collecting and rearing. Also, the author owes Drs. Hiroshi HARA, Fumio MAEKAWA, Sumihiko HATSUSHIMA, Hiroyoshi ÔHASHI, Yukiko KUROSAWA, Chang Kiaw LAN and Ding HOU for identification of larval foodplants. The Yokohama Plant Quarantine Office of the Ministry of Agriculture and Forestry (now Ministry of Agriculture, Forestry and Fisheries) favoured the author with expedient procedures in importation of living insects of foreign origin.

References

ACKERY, P. R., 1975. A guide to the genera and species of Parnassiinae (Lepidoptera: Papilionidae). *Bull. Brit. Mus. (nat. Hist.)*, **31**: 73–106.

BRYK, F., 1934. Lepidoptera, Baroniidae, Teinopalpidae, Parnassiidae. Pars I. Tierreich, **64**: xxii+131 pp.

EHRLICH, P. R., 1958. The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). *Kans. Univ. Sci. Bull.*, **39**: 305–370.

EIDMANN, H., 1930. Morphologische und physiologische Untersuchungen am weiblichen Genitalapparat der Lepidopteren. 1. Morphologische Teil. *Z. ang. Ent.*, **15**: 1–66.

FORD, E. B., 1944. Studies on the chemistry of pigments in the Lepidoptera with reference to their bearing on systematics. 3. The red pigments of Papilionidae. *Proc. R. Soc. London* (A), **19**. 4. The classification of the Papilionidae. *Trans. R. ent. Soc. London*, **94**: 201–223.

GOSSE, P. H., 1881. The prehensores of male butterflies of the genera *Ornithoptera* and *Papilio*. *Proc. R. Soc. London*, **33**: 23–27.

HIURA, I., 1980. A phylogeny of the genera of Parnassiinae on analysis of wing pattern, with description of a new genus [Lepidoptera: Papilionidae]. (In Japanese.) *Bull. Osaka Mus. nat. Hist.*, **33**: 71–95.

JORDAN, K. & STICHEL, H., 1907. Lepidopterologische Miscellen. III. Zum Heimatnachweis von *Zerynthia cerisyi* GOD. *Ent. Z. Frankf. a. M.*, **21**: 82–83.

MUNROE, E., 1960. The classification of the Papilionidae (Lepidoptera). *Canad. Ent. Suppl.*, **17**: 1–51.

PÉREZ, H., 1969. Quetotaxia y Morfologia de la Oruga de *Baronia brevicornis* SALV. *An. Inst. Biol. Univ. Nal. Autón. México, 40, Ser. Zool.*, (2): 227–244.

——— 1971. Algunas Consideraciones sobre la Población de *Baronia brevicornis* SALV. en la Región de Mezcala, Guerrero. *Ibid., 42, Ser. Zool.*, (1): 63–72.

SHIRÔZU, T., 1955. A study on foodplants of the Papilionidae in relation to evolution. (In Japanese.) *Shin Konchu*, **8** (4): 38–45, (5) 38–44, (7) 28–36.

STAUDINGER, O. & SCHATZ, E., 1885–92. Die Familien und Gattungen der Tagfalter (by SCHÄTZ, E., 1885–92; completed from 1888 by RÖBER, J.). *Ex. Schemett.*, **2** (6)+ii+292 pp., 50 pls.

TABUCHI, Y., 1974. Life histories of *Luehdorfia japonica* & *L. puziloi* in Japan. 308 pp. Tokyo.

——— 1978. The life histories of five Alpine Butterflies of the Daisetsu Mountains, Hokkaido, Japan. 459 pp. Tokyo.

TALBOT, G., 1936. Fauna of British India, Butterflies 1 (Ed. 2): 1–300. London.

VÁZQUEZ, L. & PÉREZ, H., 1961. Observaciones sobre la Biologia de *Baronia brevicornis* SALV. *An. Inst. Biol. Univ. Nal. Autón. México*, **32** (1 & 2): 295–311.

——— & ——— 1967. Nuevas Observaciones sobre la Biologia de *Baronia brevicornis* SALV. *Ibid.*, **37** (1 & 2): 195–204.

YASUMATSU, K. & TORIGATA, T., 1934. Comparative morphology of the male genital appendages of the Japanese, Corean and Formosan species of the genus *Papilio* (Lepidoptera, Papilionidae). *Zephyrus.*, **5** (4): 213–238. (In Japanese.)

ZEUNER, F. E., 1943. Studies in the systematics of the genus *Troides* HÜBNER (Lepidoptera Papilionidae) and its allies; distribution and phylogeny in relation to the geological history of the Australasian Archipelago. *Trans. zool. Soc. London*, **25**: 107–184.

摘　　要

幼生期形態に主眼を置いたアゲハチョウ科の分類 (五十嵐　邁)

アゲハチョウ科について従来行われてきた分類は，主として成虫の形態によるものであった．分類の

完全を期するためには幼生期の形態を研究することが重要であるが，広く世界に分布する異なった属の幼虫を入手することの困難さがこの研究を阻んでいた．幸いに，筆者は海外にその材料を求める機会に恵まれ，2，3をのぞいてほとんどの属についてその幼生期の形態を調査した．本論文では，各属について卵，1齢幼虫，2～終齢幼虫，蛹の形態，成虫の顕著な特徴，幼虫の食草などについて記述し，必要に応じて図示した．さらに幼生期の資料をもとに，従来の分類に検討を加えることができた．その結果，次のような法則性のあることを見いだした．

1. 1齢幼虫の外部形態が単純なものは原始的な種であり，複雑なものは進化した種と考えられる．すなわち，原始的な種では体上の一次刺毛数が少なく，進化するにしたがってその数を増す．しかし，頭部刺毛にはこの法則は適用できない．また原始的な種では体上に突起もみとめられない．

2. 1齢期から終齢期までの全幼虫期間を通じて，形態的変化の著しいものは進化したものと考えられる．

3. 1齢期から終齢期までの全幼虫期間を通じて，形態的変化の速度の速いものは進化したものと考えられる．

4. 食性については，ウマノスズクサ科を摂食するものが最も原始的で，次いでミカン科，モクレン科，クスノキ科の順に進化する．

結論として，従来のアゲハチョウ科の分類に対する新解釈として，

1. *Cressida*, *Euryades* 両属を最も原始的とする説を否定し，*Luehdorfia*, *Parnalius* 属を最も古いものとする．

2. 従来，幼生期が未知であったため，分類学的地位の定まらなかった *Meandrusa* をアゲハチョウ族に属せしめ，*Menelaides* 属よりも進化した位置を与える．

3. 従来，その位置に関して定説のなかった *Graphium* 属は，あらゆる観点から最も進化したものであることを確認する．